

The Journal of Raptor Research

Volume 38 Number 3 September 2004



Published by
The Raptor Research Foundation, Inc.

THE RAPTOR RESEARCH FOUNDATION, INC.
(FOUNDED 1966)

<http://biology.boisestate.edu/raptor/>

OFFICERS

PRESIDENT: BRIAN A. MILLSAP
VICE-PRESIDENT: DAVID M. BIRD

SECRETARY: JUDITH HENCKEL
TREASURER: JIM FITZPATRICK

BOARD OF DIRECTORS

NORTH AMERICAN DIRECTOR #1:
JEFF SMITH
NORTH AMERICAN DIRECTOR #2:
GARY SANTOLO
NORTH AMERICAN DIRECTOR #3:
TED SWEM
INTERNATIONAL DIRECTOR #1:
BEATRIZ ARROYO
INTERNATIONAL DIRECTOR #2:
RUTH TINGAY

INTERNATIONAL DIRECTOR #3:
STEVE REDPATH
DIRECTOR AT LARGE #1: JEMIMA PARRY-JONES
DIRECTOR AT LARGE #2: EDUARDO INIGO-ELIAS
DIRECTOR AT LARGE #3: MICHAEL W. COLLOPY
DIRECTOR AT LARGE #4: CAROL MCINTYRE
DIRECTOR AT LARGE #5: JOHN A. SMALLWOOD
DIRECTOR AT LARGE #6: DANIEL E. VARLAND

EDITORIAL STAFF

EDITOR: JAMES C. BEDNARZ, Department of Biological Sciences, P.O. Box 599, Arkansas State University, State University, AR 72467 U.S.A.

ASSOCIATE EDITORS

JAMES R. BELTHOFF
CLINT W. BOAL
CHERYL R. DYKSTRA
MICHAEL I. GOLDSTEIN
JOAN L. MORRISON

JUAN JOSÉ NEGRO
MARCO RESTANI
FABRIZIO SERGIO
IAN G. WARKENTIN
JAMES W. WATSON

BOOK REVIEW EDITOR: JEFFREY S. MARKS, Montana Cooperative Research Unit, University of Montana, Missoula, MT 59812 U.S.A.

SPANISH EDITOR: CÉSAR MÁRQUEZ REYES, Instituto Humboldt, Colombia, AA. 094766, Bogotá 8, Colombia
EDITORIAL ASSISTANTS: JENNIFER L. NORRIS, JOAN CLARK

The Journal of Raptor Research is distributed quarterly to all current members. Original manuscripts dealing with the biology and conservation of diurnal and nocturnal birds of prey are welcomed from throughout the world, but must be written in English. Submissions can be in the form of research articles, short communications, letters to the editor, and book reviews. Contributors should submit a typewritten original and three copies to the Editor. All submissions must be typewritten and double-spaced on one side of 216 × 278 mm (8½ × 11 in.) or standard international, white, bond paper, with 25 mm (1 in.) margins. The cover page should contain a title, the author's full name(s) and address(es). Name and address should be centered on the cover page. If the current address is different, indicate this via a footnote. A short version of the title, not exceeding 35 characters, should be provided for a running head. An abstract of about 250 words should accompany all research articles on a separate page.

Tables, one to a page, should be double-spaced throughout and be assigned consecutive Arabic numerals. Collect all figure legends on a separate page. Each illustration should be centered on a single page and be no smaller than final size and no larger than twice final size. The name of the author(s) and figure number, assigned consecutively using Arabic numerals, should be pencilled on the back of each figure.

Names for birds should follow the A.O.U. Checklist of North American Birds (7th ed., 1998) or another authoritative source for other regions. Subspecific identification should be cited only when pertinent to the material presented. Metric units should be used for all measurements. Use the 24-hour clock (e.g., 0830 H and 2030 H) and "continental" dating (e.g., 1 January 1999).

Refer to a recent issue of the journal for details in format. Explicit instructions and publication policy are outlined in "Information for contributors," *J. Raptor Res.*, Vol. 37(4), and are available from the editor. Submit manuscripts to J. Bednarz at the address listed above.

COVER: Migrating Golden Eagle (*Aquila chrysaetos*). Painting by Julie Zickefoose; for more information and images, visit www.juliezickefoose.com

CONTENTS

MODELING RAPTOR MIGRATION PATHWAYS USING A FLUID-FLOW ANALOGY. David Brandes and Daniel W. Ombalski	195
ENVIRONMENTAL CORRELATES OF AFRICAN WOOD-OWL CALLING ACTIVITY IN KIBALE NATIONAL PARK, UGANDA. Nathaniel E. Seavy	208
DIETS AND FORAGING BEHAVIOR OF NORTHERN SPOTTED OWLS IN OREGON. Eric D. Forsman, Robert G. Anthony, E. Charles Meslow, and Cynthia J. Zabel	214
A COMPARISON OF BARRED AND SPOTTED OWL NEST-SITE CHARACTERISTICS IN THE EASTERN CASCADE MOUNTAINS, WASHINGTON. Joseph B. Buchanan, Tracy L. Fleming, and Larry L. Irwin	231
PRODUCTIVITY AND NEST-SITE CHARACTERISTICS OF GRAY HAWKS IN SOUTHERN ARIZONA. Brent D. Bibles and R. William Mannan	238
JUVENILE GROUSE IN THE DIET OF SOME RAPTORS. Vitali Reif, Risto Tornberg, and Kauko Huhtala	243
VARIATION IN MITOCHONDRIAL DNA OF FOUR SPECIES OF MIGRATORY RAPTORS. Elise V. Pearlstine	250
NESTING BIOLOGY AND DIET OF THE MADAGASCAR HARRIER (<i>CIRCUS MACROSCELES</i>) IN AMBOHITANTELY SPECIAL RESERVE, MADAGASCAR. Lily-Arison Rene de Roland, Jeanneney Rabearivony, Ignace Randriamanga, and Russell Thorstrom	256
BREEDING BIOLOGY OF THE GREY-FACED BUZZARD (<i>BUTASTUR INDICUS</i>) IN NORTHEASTERN CHINA. Wen-Hong Deng, Wei Gao, and Jiang Zhao	263
SHORT COMMUNICATIONS	
VARIABLE RETENTION TIMES FOR RECTRICES AT DIFFERENT LOCI IN A GOLDEN EAGLE. David H. Ellis and Marc Kéry	270
A LOCAL CONCENTRATION OF SNOWY OWLS ON THE YUKON-KUSKOKWIM DELTA IN SUMMER 2000. Christopher M. Harwood, Brian J. McCaffery, Fred J. Broerman, and Paul A. Liedberg	275
PREMIGRATORY COMMUNAL ROOSTS OF THE LESSER KESTREL IN THE BOREAL SUMMER. Pedro P. Olea, Rubén Vera, Ángel de Frutos, and Hugo Robles	278
ANALYSIS OF THE AUTUMN MIGRATION OF JUVENILE HONEY-BUZZARDS (<i>PERNIS APIVORUS</i>) ACROSS THE CENTRAL MEDITERRANEAN. Nicolantonio Agostini, Charles Coleiro, and Michele Panuccio	283
LETTERS	
DO EURASIAN HOBBIES (<i>FALCO SUBBUTEO</i>) HAVE "FALSE EYES" ON THE NAPE? Juan José Negro, Juan Manuel Grande, and José Hernán Sarasola	287
VULTURE WINTER ROOST ABANDONMENT AND REESTABLISHMENT. Keely T. Roen and Richard H. Yahner	288
COMMENSAL FORAGING BY A RED-SHOULDERED HAWK (<i>BUTEO LINEATUS</i>) WITH WILD TURKEYS (<i>MELEAGRIS GALLOPAVO</i>). Gary R. Graves	290
NOTES ON A RANGE EXPANSION AND SUMMER DIET OF THE MOUNTAIN CARACARA IN THE ANDES OF SOUTH-CENTRAL CHILE. Ricardo Figueroa Rojas, Sergio Alvarado Orellana, and E. Soraya Corales Stappung	290
AN EXAMPLE OF COOPERATIVE HUNTING BY SAKER FALCONS IN HUNGARY. Wade L. Eakle, Carl Millier, Pierre Mineau, and János Világosi	292
BOOK REVIEW. Edited by Jeffrey S. Marks.....	294

THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 38

SEPTEMBER 2004

No. 3

J. Raptor Res. 38(3):195–207

© 2004 The Raptor Research Foundation, Inc.

MODELING RAPTOR MIGRATION PATHWAYS USING A FLUID-FLOW ANALOGY

DAVID BRANDES¹

Lafayette College, Easton, PA 18042 U.S.A.

DANIEL W. OMBALSKI

US Filter, Inc., State College, PA 16801 U.S.A.

ABSTRACT.—We describe an approach to mathematical modeling of raptor migration under conditions in which terrain updrafts are the primary source of lift. The model is based on the analogy of laminar fluid flow to raptor migration, with the assumption that migration flux at a particular location is proportional to terrain conductivity and the local energy gradient driving migration. The terrain conductivity parameter is taken to be the relative updraft strength, which is calculated using wind direction, terrain slope, and terrain aspect data determined from a digital-elevation model of the area of interest. By imposing a directional energy gradient (a preferred axis of migration [PAM]) across the resulting conductivity field, flow (i.e., migration) is generated, and the predominant migration paths through the region are determined. We apply the model by simulating the spring migration of Golden Eagles (*Aquila chrysaetos*) through central Pennsylvania under eight different wind scenarios. The locations of the simulated migration tracks depended on wind direction, PAM direction, and the spatial arrangement and orientation of terrain features. Migration tracks showed a marked tendency to converge toward a small number of preferred pathways as the migration proceeds. The overall pattern of simulated migration was consistent with available count data. Model results showed that south/southeast and north/northwest winds provided the best conditions for rapid migration across the region, as was suggested by field data.

KEY WORDS: *Golden Eagle; Aquila chrysaetos; migration; pathways; modeling; updrafts; terrain.*

MODELACIÓN DE LAS RUTAS DE MIGRACIÓN MEDIANTE EL USO DE UN MODELO DE ANALOGÍA DE FLUIDO DE FLUJO

RESUMEN.—Describimos un enfoque para la modelación matemática bajo condiciones en las cuales las corrientes térmicas son la fuente primaria para elevarse. El modelo está basado en la analogía del flujo laminar aplicado a la migración de rapaces asumiendo que el flujo migratorio en una localidad particular es proporcional a la conductividad del terreno y el gradiente de energía local que guía la migración. El parámetro de conductividad del terreno es asumido como la fuerza relativa de las corrientes ascendentes el cual es calculado usando la dirección del viento, la pendiente del terreno, determinados a partir de un modelo de elevación digital del área de interés. Mediante la imposición de un gradiente direccional de energía (un eje seleccionado de migración) a través del campo de conductividad resultante, el flujo (migración) es generado, y las rutas de migración son determinadas a través de la región. Aplicamos el modelo para simular la migración de primavera del águila dorada (*Aquila chrysaetos*) a través del centro del Pennsylvania bajo ocho escenarios de vientos diferentes. Las localidades de simulación de las rutas dependieron de la dirección del viento, del eje de migración y del arreglo espacial y de la orientación de las características del terreno. Las rutas de migración

¹ E-mail address: brandesd@lafayette.edu

mostraron una marcada tendencia hacia la cobertura de un pequeño número de rutas preferidas tal como la migración ocurre. El patrón general de la migración simulada es consistente con los datos de los conteos disponibles. Los resultados del modelo demuestran que los vientos sur/sureste y norte/noreste proveen las mejores condiciones para una rápida migración a través de la región tal como lo sugieren los datos del campo.

[Traducción de César Márquez]

It is widely held among raptor biologists and hawk watchers that some mountain ridges concentrate raptors in greater numbers than others (e.g., Haugh 1974). Why this is true is an interesting question, especially in areas like the northern Appalachians, where there is a network of ridges and many hawk watches where counts have been conducted (Zalles and Bildstein 2000). The factors that concentrate migrant raptors on one ridge, while leaving a nearby ridge of similar morphology with few migrants, have only been discussed in a qualitative sense. Detailed quantitative modeling of topographic and landscape structure effects on raptor-migration pathways at the regional scale has not been conducted.

Here we describe a raptor migration model based on a fluid-flow analogy and digital-elevation data. The overall premise is that raptors migrating over the landscape are analogous to fluid flowing through a variably conductive medium. Fluid flows are driven by directionally-oriented energy gradients, much as raptors are driven by an innate urge to migrate in a particular direction, termed the preferred axis of migration (PAM; Kerlinger 1989). Fluid flows tend to channel along connected pathways of high conductivity (i.e., "the path of least resistance"). Similarly, raptors use pathways along which migration can be obtained at the lowest energy cost, by using thermals, ridge updrafts, and other sources of lift (Kerlinger 1989). Productive inland count sites like Hawk Mountain, PA (Broun 1935) and the Goshute Mountains, NV (Hoffman 1985), are often on long or converging geographic features known as "leading lines" (Mueller and Berger 1967). In our analogy, these can be thought of as thin layers of sand (high conductivity) in an otherwise silty or clayey medium (low conductivity). Because the equations of groundwater flow are well developed, the analogy is useful in creating a quantitative model of raptor migration.

The model is applicable to conditions where updrafts or deflection currents resulting from horizontal surface winds deflecting off sloping terrain are the primary source of lift, rather than thermals or other ephemeral atmospheric phenomena dis-

cussed by Haugh (1974). Updrafts are often the primary source of lift during early spring and late fall migration in temperate latitudes, and on overcast days. We apply the model to simulate the early spring Golden Eagle (*Aquila chrysaetos*) migration through central Pennsylvania and determine its primary migration pathways through the region. The paper concludes with a discussion of the utility, limitations, and possible additional applications of the model.

METHODS

Model Equations. Fluid flows are modeled with the continuity equation (mass conservation) and a momentum equation or equation of motion. Continuity also applies to migrating raptors, meaning that the same number of raptors arrives at a location as leaves that location. For laminar flow (e.g., groundwater flow), the equation of motion is linear and is known as Darcy's law (Bear 1972):

$$q_s = K \frac{\partial h}{\partial s} \quad (1)$$

where q_s is the flux velocity (dimensions of length [L]/time [T]) in the s -direction (s is a spatial coordinate x , y , or z having dimension L), K is the hydraulic conductivity (dimensions of L/T), a material property which describes the ease of flow, and h is the fluid energy per unit weight (the symbol h is used because energy is expressed as an equivalent height (h) of water with dimension L). Restated in words, the velocity of fluid in a particular direction is directly proportional to the local conductivity (K) and the energy gradient in that direction. Analogous equations describe a variety of physical transport phenomena (e.g., heat, electricity).

The first assumption in our model is that an equation of the same form applies for raptor migration; that is, migration velocity at a particular location is directly proportional to "terrain conductivity" (defined below), and the magnitude of the local energy gradient driving migration. Clearly, raptor migration is complex and quite possibly nonlinear, but it is not unreasonable to assume this form as a first approximation. For example, migration should be rapid where terrain conductivity is high in the desired direction (i.e., the PAM) and the energy gradient (i.e., urge to migrate) is strong. Conversely, migration should be slow where terrain conductivity is low and the energy gradient is weak. Other combinations of conductivity and energy lead to intermediate migration rates.

In groundwater flows (and presumably raptor migration across a diverse landscape), the parameter K is high-

ly variable in space and may range over several orders of magnitude. For simulating flow through such a domain, it is necessary to divide the region of interest into a grid of conductivity values, and approximate the derivative term in equation (1) ($\partial h/\partial s$) by difference at each point. For example, the velocity from point i to point j was written as:

$$q_{i-j} = K_{i-j} \frac{h_i - h_j}{s_i - s_j} \quad (2)$$

where K_{i-j} is a mean conductivity for flow between points i and j (it is standard practice in groundwater modeling to use the harmonic mean, because the range of variation between gridpoints is typically quite large). Note that if $h_i > h_j$, the flux calculated from (2) will be positive; however, if $h_j > h_i$, the flux calculated from (2) will be negative, meaning that velocity (migration) is in the opposite direction (from j to i). Thus, equation (2) gives the direction of flow as well as its rate.

Now consider a gridpoint (point 0) surrounded by four gridpoints (points 1–4) an equal distance away in the east-west and north-south directions. The continuity equation for point 0 is written as:

$$q_{0-1} + q_{0-2} + q_{0-3} + q_{0-4} = 0 \quad (3)$$

Substituting equation (2) into equation (3), and solving for the energy at point 0 gives:

$$h_0 = \frac{h_1 K_{0-1} + h_2 K_{0-2} + h_3 K_{0-3} + h_4 K_{0-4}}{K_{0-1} + K_{0-2} + K_{0-3} + K_{0-4}} \quad (4)$$

When equation (4) is written for all the gridpoints in the model domain, the result is a set of algebraic equations that can be solved simultaneously (a variety of matrix solution methods can be used) for the unknown energy values.

To apply the model, a directional energy gradient is created to drive the flow by assigning different energy values to the model boundaries (for example, a higher value on the southern boundary will cause northward flow). The magnitude of this applied energy gradient relates to the biological drive to migrate, and thus, is difficult to quantify. However, to the extent that relative differences in fluxes or velocities between locations are desired rather than the flux value at each location, the magnitudes of the boundary energy values are essentially arbitrary, so long as these values create flow in the desired direction. Throughout the paper we are interested in such relative differences in migration and do not attempt to predict actual numbers of migrants.

The Conductivity Field. The second assumption in our model is that the conductivity (K), or ease of migration, at a particular location on the landscape is given by the updraft strength, which can be parameterized from the terrain orientation and slope, and direction of surface winds. Empirical support for the correlation between updraft strength and migrant airspeed is given by Kerlinger (1989). He found that lift (wind component perpendicular to the ridge) was the most important predictor of air speed for raptors migrating along the Kittatinny Ridge at Hawk Mountain, PA and Raccoon Ridge, NJ.

Updrafts will be strong where wind is perpendicular to the terrain and the terrain is steeply sloped and weak where the wind is parallel to the terrain, or the terrain

is relatively flat. For a particular wind direction, we use the product of two parameters to determine the relative updraft strength (conductivity) at each location: (1) the cosine of the angle between the terrain aspect and the wind direction (ranging from 0 for parallel winds to 1 for perpendicular winds), and (2) the terrain slope. This algorithm determines the relative conductivity of different points of the landscape as a function of wind direction. In general, steeply sloping ridges that are oriented perpendicular to the wind direction will provide connected areas of high conductivity.

The calculations can be performed using a digital-elevation model of the area of interest. A digital-elevation model is a two-dimensional matrix of elevations representing a topographic map. At each gridpoint, the local terrain aspect and slope can be determined by calculating the maximum slope value from the eight principal directions (north, northeast, east, southeast, south, southwest, west, and northwest). Because the cosine of the terrain/wind angle becomes negative where the terrain slopes away from the wind, resulting in negative conductivity, it is necessary to correct these off-wind values to zero or a small positive value (conductivity cannot be <0). Note that in reality, lift may exist due to vertical eddies on the off-wind side of a ridge; however, such turbulent features are beyond the scope of the model. The resulting grid of conductivity values (one value for each point of the digital-elevation model) serves as the connection between the migration model and the modeled region.

Interpretation of Results by Particle Tracking. Once the matrix of equations is solved, equation (2) can be used to determine the magnitude and direction of the migration flux at each gridpoint in the domain. A useful final step is to conduct “particle tracking” to trace out individual migration paths through the domain. Particle tracking is often used in fluid mechanics to help visualize and interpret complex flow fields. There are several possible algorithms for particle tracking; a simple form consists of using equation (2) to calculate the velocity in the eight possible directions from a starting point and then choosing the next cell in the highest velocity direction (termed the D8 method; O’Callaghan and Mark 1984). The calculation is repeated from the new cell, and then continued until a model boundary is eventually reached. One can also determine the travel time or velocity of a particular path through the flow field as part of the tracking algorithm.

Model Application. In this paper we apply the model to simulate the spring Golden Eagle migration through Pennsylvania. This season, species, and location were chosen as an initial test for the model because the migration occurs during a period of minimal thermal lift, count data are available for comparison with model simulations, and the flight occurs through a relatively small region of highly-variable terrain. To test the model, we summarized Golden Eagle data from spring hawk watches in northeastern North America, separated into full-time and part-time sites (Table 1). Recent full-time count data from Tussey Mountain hawk watch, 11 km southwest of State College, PA, show a substantially larger spring Golden Eagle flight than at the long-term Lake Ontario shoreline sites. Data from other part-time sites in the

Table 1. Summary of spring Golden Eagle migration count data, northeast North America. Based on data reported in *Hawk Migration Association of North America Hawk Migration Studies* and BIRDHAWK (listserv.arizona.edu/archives/birdhawk.html). Hawk Mountain data provided by L. Goodrich (pers. comm.).

SITE NAME	DESCRIPTION	LOCATION	YEARS	ANNUAL COUNT MAXIMUM	
				RANGE (MEAN)	DAILY COUNTS ^a
Full-time sites					
Braddock Bay, NY	Lake Ontario shore	Central NY	1979–2002	6–53 (22)	11, 9, 7
Derby Hill, NY	Lake Ontario shore	Central NY	1980–2002	13–92 (31)	25, 23, 16
Niagara Peninsula	Niagra Escarp./Penin.	Southern ON	1980–2002	3–13 (7)	4, 4, 3
Raccoon Ridge, NJ	Ridge	Northwest NJ	1975–76	1–3 (2)	1, 1, 1
Ripley, NY	Lake Erie shore	Western NY	1987–99	2–12 (4)	7, 3, 2
Tussey Mountain, PA	Ridge	Central PA	2001–02	119–166 (143)	22, 22, 14
Part-time sites					
Allegheny Front, PA	Edge of Allegheny Plateau	Southwest PA	1990–2002	2–75	22, 21, 19
Hawk Mountain, PA	Kittatinny Ridge	Eastern PA	1969–2002	0–2	2, 1, 1
Hook Mountain, NY	Hudson River bluff	Eastern NY	1976–2002	0–5	5, 1, 1
Jacks Mountain, PA	Ridge	Central PA	1995–99	1–11	10, 8, 3
Mount Pleasant, NY	Allegheny Plateau	West central NY	1992–93	6–34	10, 8, 3
Second Mountain, PA	Ridge	East central PA	1993–97	0–2	1, 1, 1
Sideling Hill, PA	Ridge	South central PA	1997–98	18–43	15, 5, 5
Tuscarora Summit,	Ridge	South central PA	1977–2002	0–9	3, 2, 2
Tussey Mountain, PA	Ridge	Central PA	1995–2000	16–95	20, 16, 15
Valleyfield, QE	River crossing	Southern QE	1980–2002	2–55	19, 8, 5
White Deer Ridge, PA	Ridge	Central PA	2000–01	25–33	13, 11, 6

^a The three highest counts on record are listed.

western portion of the ridge-and-valley region suggest similar numbers of migrating Golden Eagles. However, Golden Eagles are rarely seen along the Lake Erie and Lake Ontario shorelines to the northwest, or along the Kittatinny Ridge to the east. Based on a comprehensive review of such data, Brandes (1998) suggested a narrow spring migration route through the ridges of central Pennsylvania west of Harrisburg, which is distinct from the fall migration route across the state, documented extensively at hawk watches along the Kittatinny Ridge (e.g., Hawk Mountain, Waggoner’s Gap). Available satellite telemetry data (Brodeur et al. 1996) are consistent with a spring route through central Pennsylvania. Approximately 80% of the spring Golden Eagle flight at Tussey Mountain occurs from late February through March with a median date of 10 March, and only 11 of 285 Golden Eagles for which flight path data were recorded during spring 2001 and 2002 were crossing and leaving the ridge (D. Ombalski, D. Brandes, and M. Lanzone unpubl. data). Thus, the model assumption that eagles primarily use terrain updraft-dominated lift is reasonable for this application.

To create the conductivity field for simulating spring Golden Eagle migration through Pennsylvania, we used the 1:250 000 scale (ca. 100-m resolution) state digital-elevation model available from the United States Geological Survey (<http://edc.usgs.gov/geodata/>). Higher resolution data are available, but are unnecessary for

simulating migration over scales of several hundred kilometers. Mountain ridges in this region are on the order of 2–3 km wide, therefore such terrain features are well represented at the 100-m resolution. The size of the digital-elevation model (2860 × 4950 gridpoints for the entire state) requires that the equations be solved at more than 14 million locations; to reduce the computer memory requirements, we focused on a 2400 × 2400 grid (240 km × 240 km) of the central portion of Pennsylvania (Fig. 1) where Golden Eagles are known to migrate. Satellite telemetry data from the eastern U.S. (Brodeur et al. 1996) gave an average spring migration distance of 68 km/d, indicating it takes Golden Eagles several days to traverse the study region.

Note the contrasting topography of the Allegheny Plateau (northwest portion), the ridge-and-valley (central portion), and Piedmont physiographic provinces (southeast) in Fig. 1. Slopes are maximized in deeply incised canyons of the Appalachian Plateau, and along the ridges of the ridge-and-valley province. The terrain aspect through the study area is dominated by the southeast and northwest directions, due to the southwest to northeast trend of the Appalachian Mountains.

Slope and aspect at each point of the digital-elevation model were determined using the Spatial Analyst package of the ArcView Geographical Information System (Environmental Systems Research Institute, Redlands, CA U.S.A.), and the conductivity was determined using

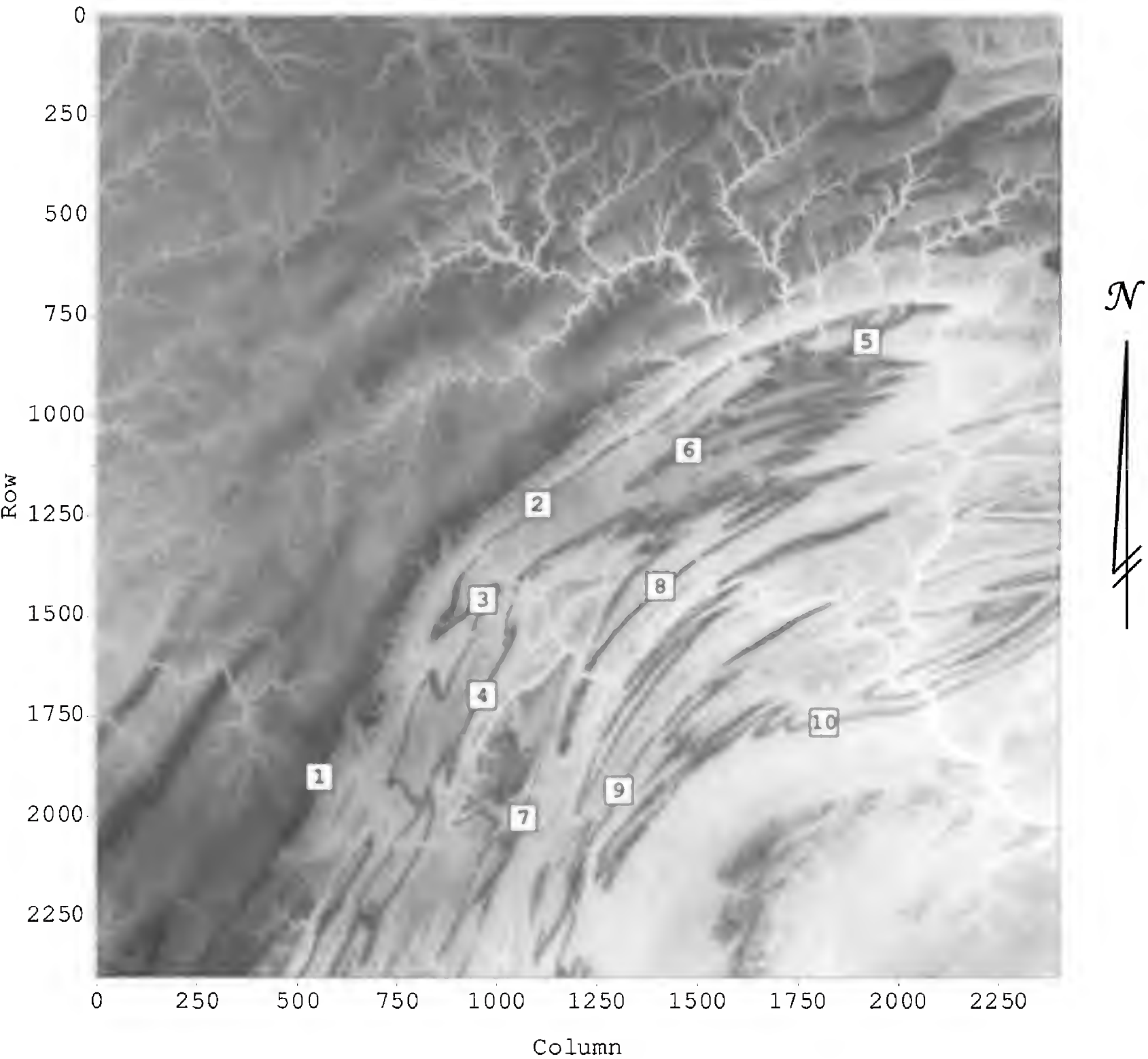


Figure 1. 100-m resolution shaded digital-elevation model (dark = high elevation, light = low elevation) of central Pennsylvania covering a 240×240 km area centered on the town of State College. Landscape features are designated by numbers: 1 = Allegheny Front, 2 = Bald Eagle Mountain, 3 = Brush Mountain, 4 = Tussey Mountain, 5 = White Deer Ridge, 6 = Nittany Mountain, 7 = Sideling Hill, 8 = Jacks Mountain, 9 = Tuscarora Mountain, 10 = Kittatinny Ridge.

the method outlined above in the Map Calculator function of ArcView. All negative conductivity values were set to a constant value of +0.01, several orders of magnitude below typical windward terrain conductivity values. We also investigated the application of a nonlinear scale factor to the conductivity values to widen their range of variation; however, this had no significant effect on the simulated migration tracks. The results were exported from ArcView as a text array for input to the model, which was implemented as a FORTRAN program. To reduce the number of required simulations, model runs were made for four combined wind directions (south/southeast,

west/southwest, north/northwest, and east/northeast) rather than all eight, by summing the respective conductivity fields. This was felt to be a reasonable approach since winds are deflected locally by the terrain and often shift over the course of a day as weather systems move across the region. To generate flow across the model domain, constant energy values were imposed along the southern (high energy) and northern (low energy) boundaries of the region to create a northward (PAM = 0°) energy gradient. We used energy values of 1000 and 0 for the south and north, respectively (we also investigated northward

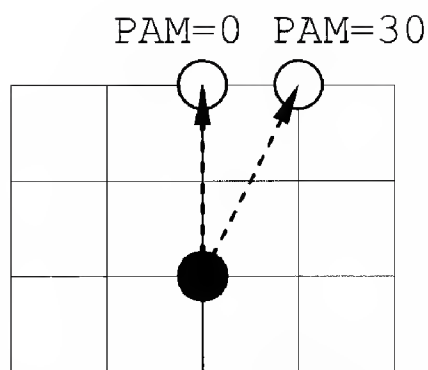


Figure 2. Schematic of imposed migration used for traversing low-velocity zones of the model domain. The migration track is deflected 200 m to the north for principal axis of migration (PAM) = 0° , and 225 m to the north-northeast for PAM = 30° .

gradients of 100–0 and 10–0, but these had no effect on the relative differences in flux values between locations or on the simulated tracks).

A 30° (north/northeast) PAM was also simulated, because spring interthermal glide directions were found to be ca. $20\text{--}30^\circ$ in central New York where leading lines are absent (Kerlinger 1989). Furthermore, relative to the spring counts in central Pennsylvania, few Golden Eagles appear along the southern shore of Lake Ontario in March (Brandes 1998), which suggests a northeastward migration heading from central Pennsylvania. This was implemented by imposing an additional set of constant energy values to the north and south boundaries incorporating the 30° deflection.

Once the flow field was solved, particle tracking was done from a series of equally spaced points along a portion of the southern boundary of the model (column 200–1100 at 50 column [5 km] increments; Fig. 1). This 90-km span encompasses the region where hawk-watch data show that Golden Eagles enter Pennsylvania during spring migration (Brandes 1998). We note that the distribution of Golden Eagles entering Pennsylvania is almost certainly nonuniform; thus each starting point represents different numbers of migrants. The maximum velocity tracking algorithm described previously was used throughout. For each track, velocity data at each step was recorded so that travel times and mean velocities of different tracks could be compared.

In preliminary model runs, we found that in low-velocity regions of the model domain, such as flat terrain, this algorithm tends to produce unrealistically circuitous migration tracks and dead-ends in terrain coves and dips. Such issues are common in digital-elevation model-based analysis when the scale of terrain variation is smaller than the grid resolution, and are often solved by applying a pit-filling routine to artificially smooth the terrain (e.g., Jenson and Domingue 1988). To prevent such dead-end tracks and ensure continued migration across low conductivity regions, at each gridpoint where the maximum velocity from equation (2) dropped below a threshold velocity of 1 (typical velocities along ridges were 15 to 150), a PAM-directed migration of two gridpoints was imposed (Fig. 2). Our reasoning is that where sources of lift are lacking, raptors will expend energy to continue migrating in the desired direction.

RESULTS

Conductivity Fields. The mountain ridges create a network of high conductivity pathways relative to the surrounding terrain (Fig. 3). Although the deeply incised river valleys of the northern Appalachian Plateau also show high conductivity, these are generally not well aligned or continuous over large distances (Fig. 3). Note the similarity in the south/southeast and north/northwest fields, and the east/northeast and west/southwest fields; this reflects the general longitudinal symmetry of the ridges. There are important exceptions to this symmetry, such as the Allegheny Front (Fig. 1) on south/southeast appearing as a long streak of high conductivity that all but disappears on north/northwest winds. The ridges in the southern portion of the study area are oriented at ca. $20\text{--}25^\circ$, and show high conductivity on east/northeast and west/southwest winds (due to the east and west components, respectively). Near the center of the study area the ridges generally bend more easterly to ca. $50\text{--}60^\circ$, and thus their conductivity is much reduced on east/northeast and west/southwest winds compared to south/southeast and north/northwest winds.

Simulated Migration Tracks. Based on simulated trends there is a marked convergence of flight paths across the region, from 19 entering to 4 exiting (Figs. 4–7). The model clearly shows the influence of the ridges in directing the migration pattern, particularly for the PAM = 30° case. In many cases the simulated flight paths follow ridges for 10s of km (in some cases >100 km), including ridges such as the Allegheny Front, Tussey Mountain, Sideling Hill, and Jacks Mountain (Fig. 1). At the termination of the ridges in the northeast part of the study area for the PAM = 0° case, flight tracks bend northward across the intervening valleys, whereas for PAM = 30° , the tracks head north-northeast.

Figure 5 shows the simulated migration tracks for north/northwest wind directions. Overall, the particle tracks for north/northwest winds (Fig. 5) are similar to those on south/southeast winds, with the flight even more confined to the ridge-and-valley region. Convergence of the flight to a few paths through the central part of the study area is again apparent. For the PAM = 30° case, the flight tends more toward the eastern ridges and away from the Allegheny Plateau. The difference in PAM can be influential in changing the flight pattern at a spe-

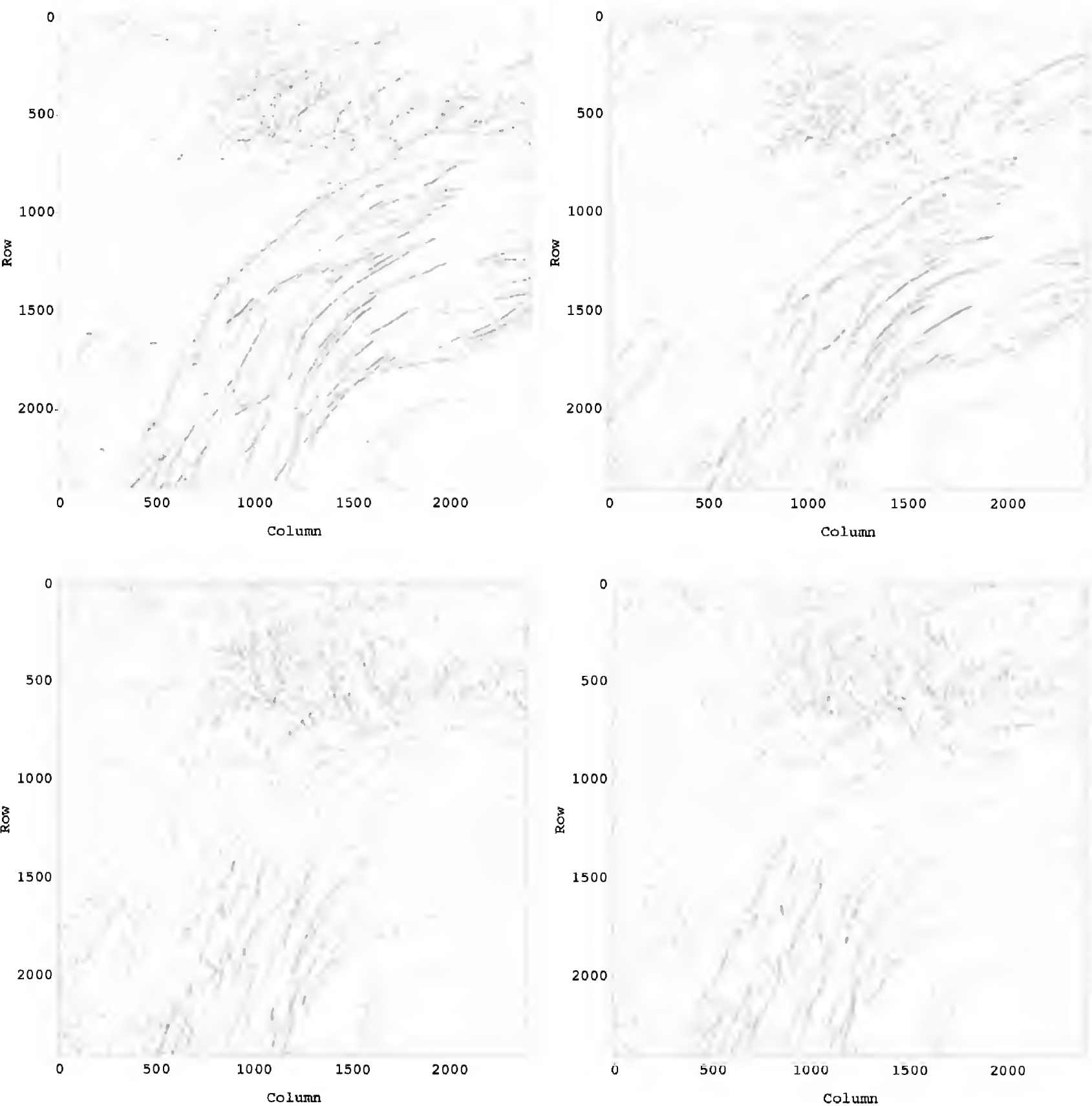


Figure 3. Relative conductivity (i.e., updraft strength) of central Pennsylvania for south/southeast winds (top left), north/northwest winds (top right), west/southwest winds (bottom left), and east/northeast winds (bottom right). Regions of high conductivity are dark and regions of low conductivity are light.

cific location, such as the northern end of Brush Mountain (Fig. 1). For $PAM = 0^\circ$, the track heads northward across the 12-km wide Nittany Valley, while for $PAM = 30^\circ$, it crosses the 5-km wide gap northeastward to Tussey Mountain. Note that this effect did not occur on south/southeast winds, showing the sensitivity to both wind direction and PAM.

The overall pattern for west/southwest wind directions (Fig. 6) trends more along the PAM under these conditions than for the south/southeast and north/northwest winds, with more tracks crossing the Allegheny Plateau, where conductivity is generally lower and the terrain is not as directionally oriented. Although there is some ridge deflection in the southern portion of the study area where

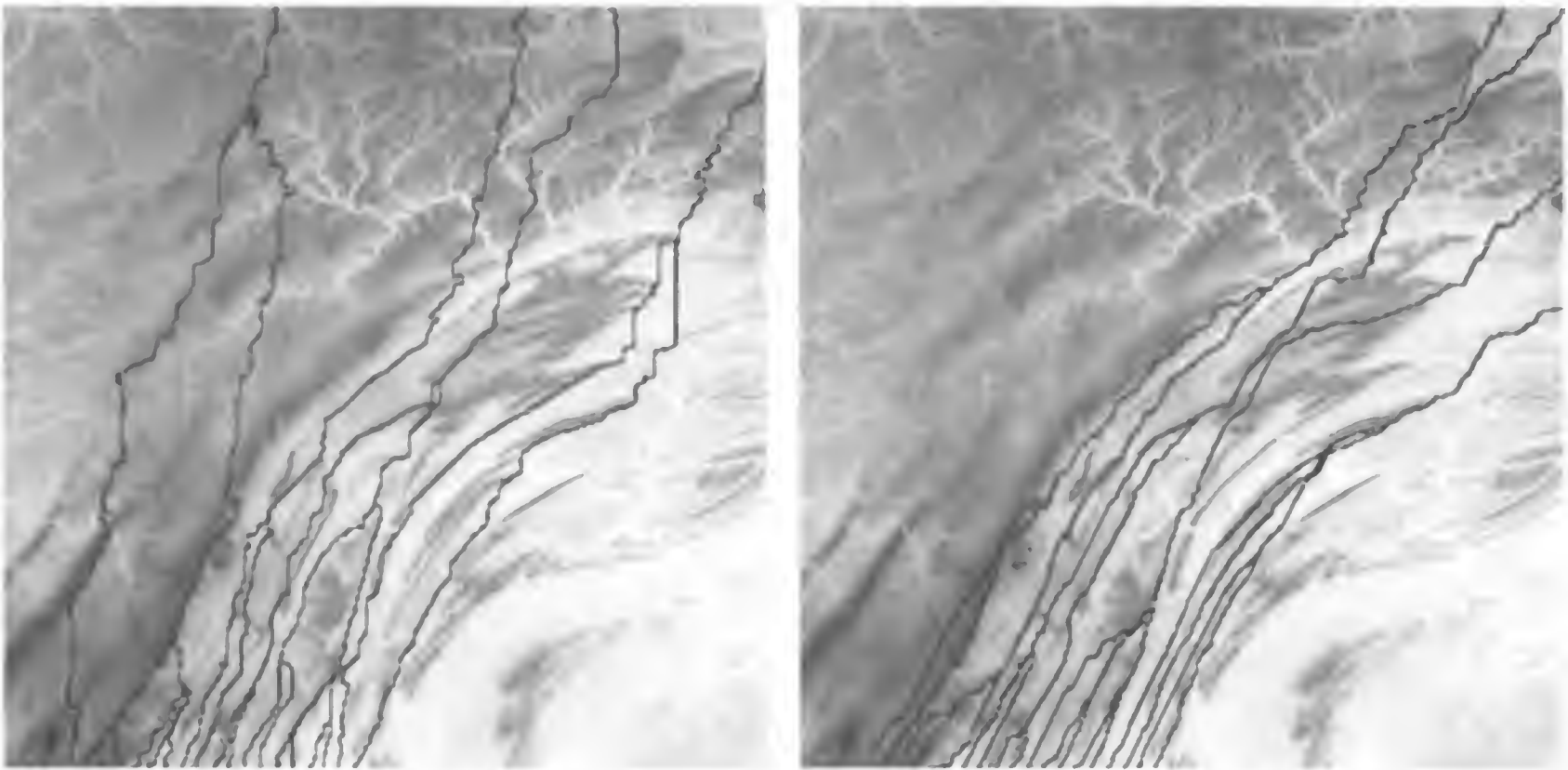


Figure 4. Simulated migration tracks through central Pennsylvania for south/southeast winds. Left image for principal axis of migration (PAM) = 0°, right image for PAM = 30°.

the ridges are oriented more northerly (20–25°), the ridges are not as effective in deflecting the migration as for the previous cases, particularly where the ridges bend eastward near the center of the study area. As a result, the convergence of flight paths is not as strong as for the south/southeast and north/northwest winds.

The model results for east/northeast wind directions (Fig. 7) are similar to those for west/southwest winds, again showing a more PAM-oriented pattern with less convergence than for south/southeast or north/northwest winds. Several tracks can be seen to cross the ridges without deflection. One dead-end track is shown in Fig. 7 (PAM =

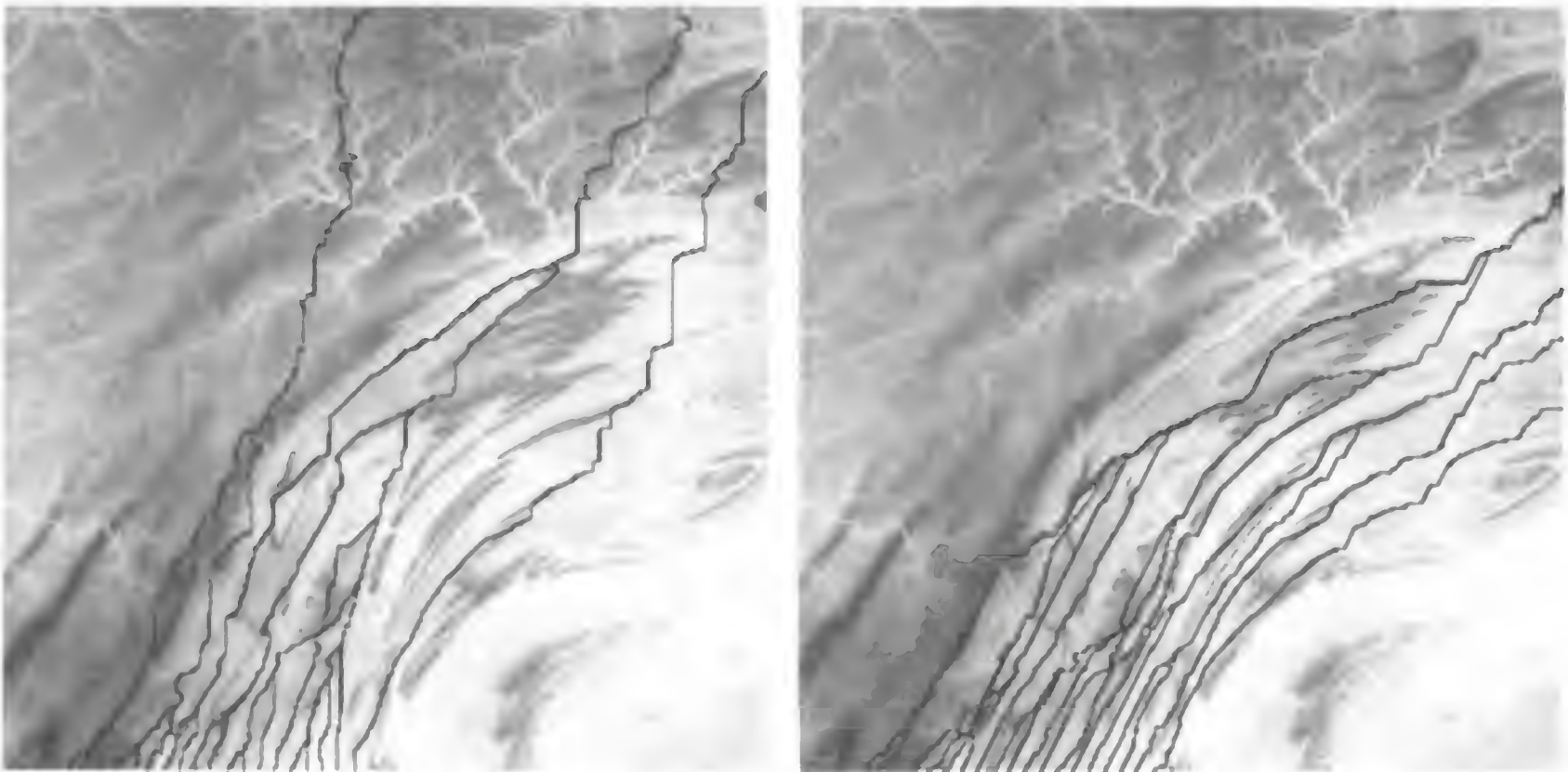


Figure 5. Simulated migration tracks through central Pennsylvania for north/northwest winds. Left image for principal axis of migration (PAM) = 0°, right image for PAM = 30°.

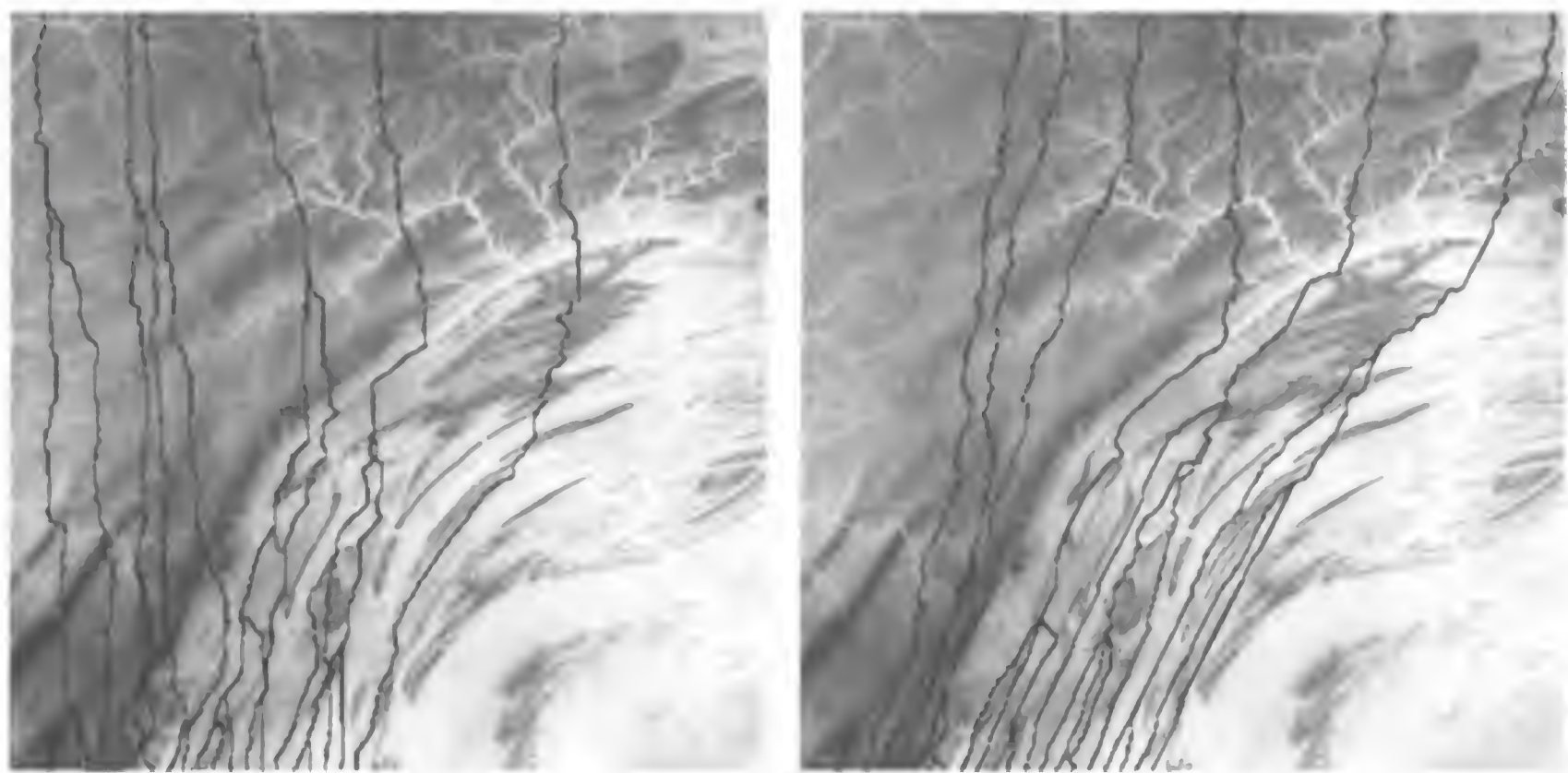


Figure 6. Simulated migration tracks through central Pennsylvania for west/southwest winds. Left image for principal axis of migration (PAM) = 0°, right image for PAM = 30°.

30°); this is a result of local “pits” in the energy field due to dips and southward-facing coves in the terrain.

For the two PAM values used, higher mean track velocities through the study area are realized on south/southeast and north/northwest winds than

on west/southwest and east/northeast winds (Table 2). This is due to the flight being more confined to high-conductivity pathways extending across the study area. A further point of interest is that the tracks that enter west of the ridge-and-valley region (west of column 500) are significantly

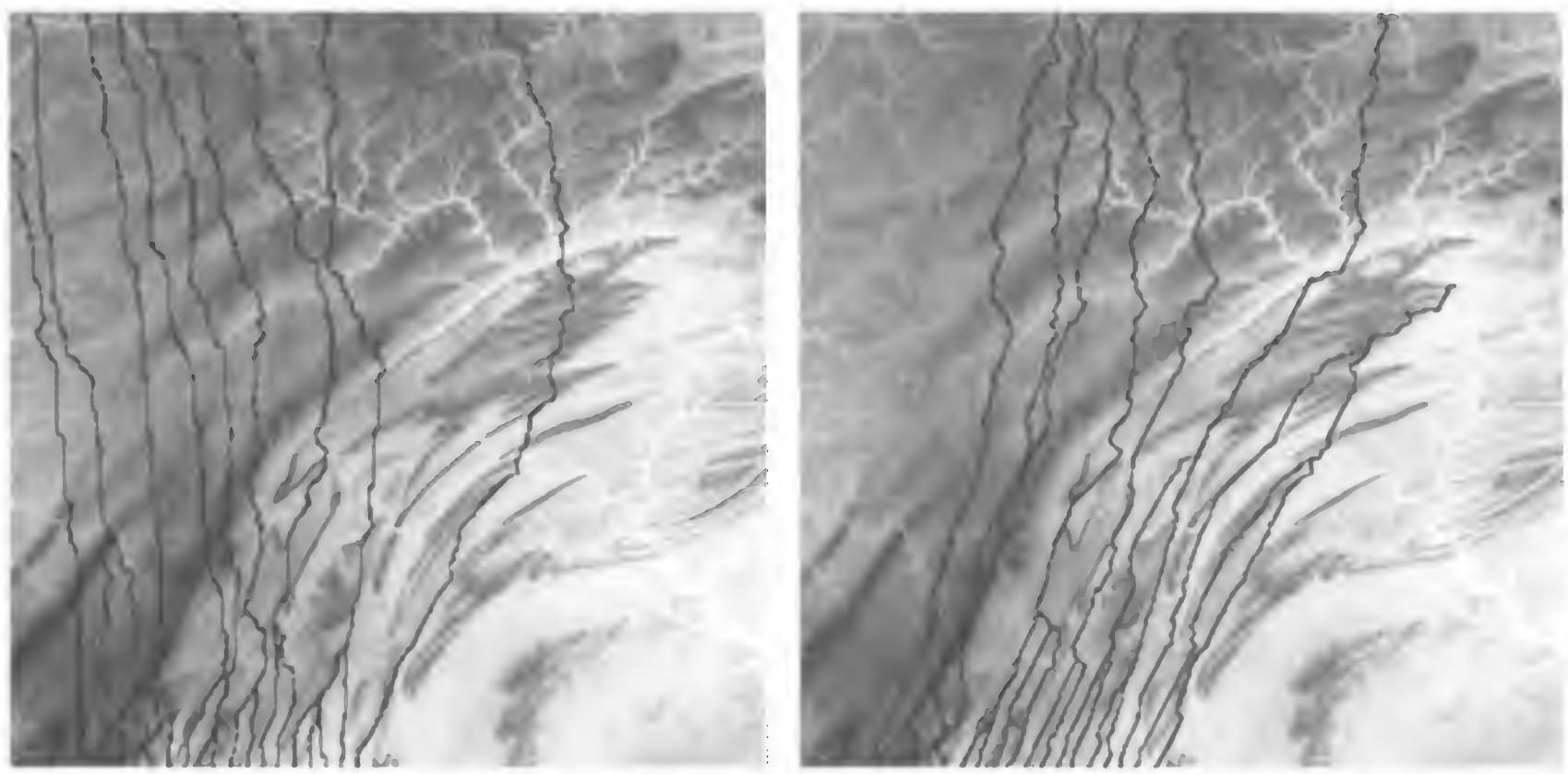


Figure 7. Simulated migration tracks through central Pennsylvania for east/northeast winds. Left image for principal axis of migration (PAM) = 0°, right image for PAM = 30°.

slower than those that enter within the ridge-and-valley region. Three particular entry areas produce the highest velocity tracks: columns 500–700, columns 850–950, and column 1100. Each of these corresponds to the locations of long parallel ridges (Fig. 1).

DISCUSSION

Simulated Migration Tracks. The model results indicated that migration patterns of raptors using terrain updrafts for lift can be simulated using digital-elevation model data and the fluid flow analogy. The particular pathways are dependent on the structure and orientation of the terrain, the wind direction, and choice of PAM. The convergence of pathways as the migration progresses is present to varying degrees in all simulations, and is the natural result of the requirement of minimum energy consumption in traversing a network of conductive pathways. This convergence effect, coupled with spatial differences in terrain conductivity, is at least partially responsible for the difference in migration counts between sites.

For the application to spring migration of Golden Eagles through central Pennsylvania, the model suggests that under south/southeast or north/northwest winds, Golden Eagles migrate through the ridge-and-valley region, and then north or northeast across the Allegheny Plateau, with convergence of pathways as migration progresses northward. Under west/southwest and east/northeast winds, the orientation of the topographic features is such that high conductivity zones are less well connected across the region, and thus the pattern is less influenced by the ridge network and less subject to pathway convergence. Furthermore, these winds result in poor lift conditions with lower mean track velocities through the study area (Table 2). This is qualitatively consistent with our experience at Tussey Mountain, where 230 of 285 Golden Eagles counted during full-time coverage in spring 2001 and 2002 were on south/southeast or north/northwest winds, and all large Golden Eagle flights ($>10/d$) have occurred on south/southeast or north/northwest winds (D. Ombalski, D. Brandes, and M. Lanzzone unpubl. data). At Tussey Mountain, south/southeast winds in early spring are usually associated with rapidly warming temperatures, and east/northeast winds are often accompanied by low pressure and rain, which may account for some of these observed differences.

The entry locations producing the highest veloc-

ity tracks (columns 500–700, columns 850–950, and column 1100) are in qualitative agreement with available count data. The first location includes two parallel ridges that converge to Tussey Mountain, the second includes two parallel ridges that converge to Sideling Hill, and the third is near the end of Tuscarora Mountain. Tussey and Sideling are both known for spring Golden Eagle migration (Table 1). Golden Eagles are uncommon migrants at Tuscarora Mountain, which is the easternmost ridge that consistently records Golden Eagles in spring (Table 1).

In no cases do simulated migration tracks follow the Kittatinny Ridge to the northeast. However, this is a direct result of the location of the chosen entry points, not a lack of updrafts along that particular ridge. Nonetheless, the simulations are consistent with field data: mean of one Golden Eagle per year is seen during the spring count at Hawk Mountain (L. Goodrich pers. comm.), and other part-time counts that have been conducted along the Kittatinny Ridge have rarely reported Golden Eagles. Thus, the model provides indirect evidence that Golden Eagles are not entering Pennsylvania to the east of Tuscarora Mountain.

The lack of Golden Eagles in spring on the southern shore of Lake Erie and the southwestern shore of Lake Ontario (Table 1) is also predicted by the model. Only two cases simulated (west/southwest winds with PAM = 0 and east/northeast winds with PAM = 0) showed migration tracks toward these areas, and these are low-velocity tracks, indicating poor lift conditions.

Although the simulated migration pattern is consistent with available data, we suspect that the model tends to overpredict convergence of flight tracks due to the deterministic tracking algorithm. Once two tracks converge, they cannot branch off because there is no stochastic or random component to the tracking algorithm. In reality, birds may leave a flight path for a variety of reasons during migration (e.g., foraging, habitat preference, to interact with other birds). Such behavior undoubtedly occurs more than the model results indicate. We chose not to include wind drift effects, although these could easily be incorporated into the tracking algorithm. Satellite tracking data across the relatively flat terrain of southern Quebec and Ontario showed that Golden Eagles can maintain a consistent heading against prevailing winds (Brodeur et al. 1996). Our observations (pers. obs.) of Golden Eagles migrating along central Pennsylva-

Table 2. Summary of mean velocities for simulated migration tracks across central Pennsylvania. The values shown have been normalized by the mean velocity of all simulated tracks.

STARTING COLUMN	PAM = 0					PAM = 30				
	SSE	NNW	WSW	ENE	MEAN ^a	SSE	NNW	WSW	ENE	MEAN ^a
200	0.33	0.63	0.37	0.28	0.40	0.76	1.24	0.28	0.26	0.64
250	1.10	0.61	0.38	0.34	0.61	1.18	1.18	0.40	0.28	0.76
300	1.08	0.57	0.37	0.48	0.63	0.78	Dead-end	0.37	0.50	0.55
350	1.07	0.63	0.32	0.53	0.64	0.81	1.44	0.30	0.50	0.76
400	0.85	0.55	0.30	0.47	0.54	0.82	1.39	0.32	0.60	0.78
450	1.00	0.54	0.33	0.43	0.58	0.84	1.31	0.32	0.74	0.80
500	0.91	2.12	1.04	0.40	1.12	1.16	1.82	1.10	1.14	1.31
550	1.12	1.64	0.67	1.02	1.11	0.96	1.64	0.53	1.12	1.06
600	1.52	1.77	1.44	0.98	1.43	1.96	1.53	0.65	0.97	1.28
650	1.93	1.77	1.46	0.60	1.44	2.01	1.34	0.73	1.08	1.29
700	1.42	1.19	1.00	1.58	1.30	1.15	1.12	0.60	0.75	0.91
750	0.86	1.20	1.06	1.15	1.07	1.02	1.15	0.67	0.75	0.90
800	0.81	1.23	0.86	1.02	0.98	1.05	1.60	0.71	0.55	0.98
850	1.56	1.26	1.66	0.92	1.35	1.34	1.45	0.99	0.77	1.14
900	1.39	1.26	1.27	1.06	1.25	1.44	1.54	1.01	1.29	1.32
950	1.52	1.15	1.20	1.22	1.27	1.68	0.57	0.36	1.17	0.94
1000	1.59	1.11	1.03	1.07	1.20	1.57	0.72	0.35	0.50	0.79
1050	1.51	1.08	1.01	0.82	1.11	0.70	1.90	0.60	0.57	0.94
1100	1.28	1.95	1.03	1.48	1.44	1.20	2.57	0.35	1.09	1.30
Mean ^b	1.20	1.17	0.88	0.83		1.18	1.42	0.56	0.77	

^a Mean velocity for a particular track across all four directions.
^b Mean velocity for a particular direction across all tracks.

nia ridges under high-wind conditions (>50 km/hr) following passage of late fall cold fronts further argues against a wind drift effect on Golden Eagle migration.

Overall, the model results demonstrate that the fluid-flow analogy and digital-elevation-model-based approach is useful for simulating raptor migration. The model yields quantitative insight into observed migration patterns through a ridge system, and helps explain why some count sites yield greater numbers than others. The model can also be used to predict sites of concentrated raptor passage, given known locations for the origin and destination of the flight.

Limitations. The ability to quantify the model results more precisely, or to test and calibrate the model, is dependent on accurate boundary conditions, that is, data on the distribution of raptors entering the modeled region. In our application, we showed migration tracks initiating from equally spaced starting points along a portion of the southern boundary, but do not have the necessary data to assign numbers of Golden Eagles to each point.

With such data, one could use the model to predict numbers of migrants at different locations within the region, which could be tested by field observation. Future simulations and model calibration will explore the effects of different raptor distributions at the model boundary.

It is clear that there are limitations to the fluid-flow analogy. Choices of migration direction are assumed to occur based on an energetic response to local conditions encountered during migration, which does not reflect the behavioral flexibility of migrating raptors. The model cannot account for the fact that a migrating eagle can see several kilometers ahead and choose its flight path based on distant landscape features; this is particularly evident in simulations where tracks go up valleys despite a nearby parallel ridge of high conductivity (especially in the case of PAM = 30°), or fail to cross a several-kilometer gap in a ridge. Klem et al. (1985) showed that >95% of migrating raptors proceeded across a 1.3-km water gap (Lehigh River) in the Kittatinny Ridge without leaving the ridge, so it is clear that a raptor's decision process

is not based strictly on local energy conditions. However, a modified tracking algorithm is under development that will search beyond adjacent grid-points to choose the direction toward the location of highest conductivity within a specified distance.

Finally, the model also does not take into account "learned" behavior. Long-lived species like Golden Eagles may develop a preferred migration route over many seasons of experience that is only partially dependent on energy minimization. Other factors may determine migration route choices, such as selection based on preferred or habitually-used habitat, prey availability, avoidance of humans, or visual cues from other migrants. In the case of Golden Eagles, the Pennsylvania ridges constitute some of the most extensive and remote woodland corridors in the region, so these high conductivity pathways may also be preferred migration routes for other such reasons. One could conceivably use habitat overlays based on geographical information system datasets as weighting or adjustment factors for the conductivity field, thus incorporating habitat considerations into the model.

Possible Applications and Extensions to the Model. The model as described here is capable of simulating the migration of a variety of diurnal raptors, so long as the basic premise of the model is met—that updrafts resulting from horizontal surface winds deflecting off sloping terrain are the dominant source of lift. This would include other late fall and early spring migrants besides Golden Eagles, or migration during overcast conditions. For smaller species, it may be necessary to incorporate a wind-drift algorithm when crossing low conductivity (flat) terrain.

Application of the model over larger spatial domains (e.g., the entire Appalachian Mountain range) is possible; however, several problems must be overcome. First, computer memory is a significant limitation, because even at much larger scales, the digital-elevation model must be of sufficient resolution to accurately represent the landscape features that affect migration. Simulation of migration over a 2000×1000 km region using the 100-m resolution data would require the processing of ca. 1.5-gigabyte computer files. Secondly, the larger the spatial scale, the more time required for migration through the model domain. This means that a realistic large-scale simulation must take into account changing wind conditions, and thus a time-varying conductivity field. However, dynamic models of thermal uplift in the atmospheric boundary layer

already exist, and could be coupled with our terrain-based updraft model and habitat data to create a raptor migration model capable of large-scale dynamic simulations. Such a model would be a valuable tool in identifying conservation priorities at the continental scale, or planning field studies in likely concentration areas where data are lacking. In addition, this type of model for a local region could be used as a predictive tool to estimate times, conditions, and locations when migrating birds present a high risk of collision with aircraft.

ACKNOWLEDGMENTS

Conversations between the authors and Mike Lanzone formed the genesis of the idea that digital terrain data might be used to model raptor migration. We thank Laurie Goodrich, Steve Hoffman, and Tim O'Connell for thoughtful comments on a draft of the paper. The review comments of Keith Bildstein and Jeff Smith also improved the final manuscript.

LITERATURE CITED

- BEAR, J. 1972. Dynamics of fluids in porous media. American Elsevier, New York, NY U.S.A.
- BRANDES, D. 1998. Spring Golden Eagle passage through the northeast U.S.—evidence for a geographically concentrated flight? *Hawk Migrat. Assoc. No. Amer. Hawk Migrat. Stud.* 23:38–42.
- BRODEUR, S., R. DECARIE, D.M. BIRD, AND M. FULLER. 1996. Complete migration cycle of Golden Eagles breeding in northern Quebec. *Condor* 98:293–299.
- BROUN, M. 1935. The hawk migration during the fall of 1934, along the Kittatinny Ridge in Pennsylvania. *Auk* 52:233–248.
- HAUGH, J.R. 1974. Local ephemeral weather conditions and their effects on hawk migration routes. Pages 72–84 in M. Harwood [ED.], Proceedings of the North American hawk migration conference 1974. Hawk Migration Association of North America, Washington, CT U.S.A.
- HOFFMAN, S.W. 1985. Raptor movements in inland western North America: a synthesis. Pages 325–338 in M. Harwood [ED.], Proceedings of hawk migration conference IV. Hawk Migration Association of North America, Rochester, NY U.S.A.
- JENSON, S.K. AND J.O. DOMINGUE. 1988. Extracting topographic structure from digital elevation data for geographical information system analysis. *Photogram. Eng. Remote Sens.* 54:1593–1600.
- KERLINGER, P. 1989. Flight strategies of migrating hawks. The University of Chicago Press, Chicago, IL U.S.A.
- KLEM, D. JR., B.S. HILLEGAS, D.A. PETERS, J.A. VILLA, AND K. KRANICK. 1985. Analysis of individual flight patterns of migrating raptors at a break in the Kittatinny Ridge: Lehigh Gap, Pennsylvania. Pages 1–11 in M. Harwood [ED.], Proceedings of hawk migration con-

- ference IV. Hawk Migration Association of North America, Rochester, NY U.S.A.
- MUELLER, H.C. AND D.D. BERGER. 1967. Wind drift, leading lines, and diurnal migration. *Wilson Bull.* 79:50–63.
- O'CALLAGHAN, J.F. AND D.M. MARK. 1984. The extraction of drainage networks from digital elevation data. *Comp. Vision, Graph. & Imaging Proc.* 28:324–344.
- ZALLES, J.I. AND K.L. BILDSTEIN (EDS.). 2000. Raptor watch: a global directory of raptor migration sites. BirdLife International, Cambridge, U.K. and Hawk Mountain Sanctuary, Kempton, PA U.S.A.

Received 3 July 2003; accepted 24 February 2004

ENVIRONMENTAL CORRELATES OF AFRICAN WOOD-OWL CALLING ACTIVITY IN KIBALE NATIONAL PARK, UGANDA

NATHANIEL E. SEAVY¹

Department of Zoology, 223 Bartram Hall, P.O. Box 118525, University of Florida, Gainesville, FL 32611 U.S.A. and Klamath Bird Observatory, P.O. Box 758, Ashland, OR 97520 U.S.A.

ABSTRACT.—Over a 1-yr period, I documented the relationship of habitat, season, lunar phase, cloud cover, and wind with patterns of African Wood-Owl (*Strix woodfordii*) calling activity in Kibale National Park, Uganda. During 10-min surveys at 10 locations, five in unlogged and five in selectively-logged tropical forest, I recorded three indices of unsolicited calling activity: whether or not owls were detected at a station, number of individuals detected, and number of vocalizations detected. African Wood-Owls were abundant in the study area and called throughout the year; I detected owls on 232 of 480 (48%) surveys. When measured by number of vocalizations detected, calling activity was greater during full moons and on clear nights, and reduced during new moons and on cloudy nights. Lunar phase and cloud cover did not have a significant effect on whether or not owls were detected or on the number of individuals detected, but nonsignificant trends were consistent using each index. These results demonstrate the importance of considering environmental factors and response variables when designing and interpreting studies that measure calling activity.

KEY WORDS: *African Wood-Owl*; *Strix woodfordii*; *Uganda*; *survey*; *vocalizations*; *cloud cover*; *lunar phase*.

CORRELACIONES AMBIENTALES DE LAS VOCALIZACIONES DE *STRIX WOODFORDII* EN EL PARQUE NACIONAL DE KIBALE, UGANDA

RESUMEN.—Durante un periodo de un año, documente la relación de hábitat, estacionalidad, fase lunar, cobertura nubosa y viento con los patrones de vocalización de *Strix woodfordii* en el Parque Nacional de Kibale, Uganda. Durante periodos de 10-minutos en 10 localidades, cinco sin tala y cinco con tala selectiva de bosque tropical, registre tres índices de vocalizaciones espontáneas: presencia/ausencia, numero de individuos y numero de vocalizaciones. Los búhos fueron abundantes en el área de estudio y vocalizaron durante todo el año. Detecte a los Búhos en 232 de los 480 (48%) muestreos. Al medir el numero de vocalizaciones encontré que esta actividad fue mayor durante las lunas llenas, en noches claras y fue menor en las lunas nuevas y noches nubladas. La fase lunar y la cobertura nubosa no tuvieron un efecto significativo para la detección de individuos, aunque las tendencias no significativas fueron consistentes al utilizar cada índice. Estos resultados demuestran la importancia de considerar los factores ambientales y los variables de respuesta cuando se diseña y se interpretan estudios que miden la actividad de vocalización.

[Traducción de César Márquez]

Variation in nighttime-calling activity of owls can be associated with lunar phase (Ganey 1990, Clark and Anderson 1997), cloud cover (Ganey 1990, Clark and Anderson 1997), wind speed (Gerhardt 1991), season (Ritchison et al. 1988, Ganey 1990), and even ecological factors, such as food abundance and mating status (Martin 1974, Lundberg 1980). Understanding these relationships can provide information about the ecological and behavioral significance of owl vocalizations.

Sampling methods used to measure calling activ-

ity of owls have varied among studies. Some studies have measured calling activity in response to a broadcast of taped conspecific vocalizations (Gerhardt 1991, Pardieck et al. 1996, Clark and Anderson 1997), whereas others have monitored spontaneous calling activity (Ganey 1990). Furthermore, these studies have used different indices as measures of calling activity. The most commonly used response variable is the number of owls detected during a survey (Clark and Anderson 1997, Pardieck et al. 1996), but other studies have analyzed either the number of calls or calling bouts (Ganey 1990) or whether or not an owl vocaliza-

¹ E-mail address: nseavy@zoo.ufl.edu

tion was detected (Gerhardt 1991). If indices of calling activity are measurably influenced by environmental factors, then apparent variation in the response of owls to environmental conditions may simply reflect differences in methodologies.

The African Wood-Owl (*Strix woodfordii*) is a common resident of forests and dense woodland throughout most of east, central, and southern Africa (Fry et al. 1988). African Wood-Owls can be monitored effectively by acoustical surveys, as demonstrated by the use of sonogram analysis to estimate density and turnover of a population in South Africa (Kemp and Kemp 1989, Delport et al. 2002). Furthermore, the vocal behavior of these owls lends itself to playback experiments that test behavioral hypotheses. However, environmental factors influencing their calling activity have not been studied. Such information is critical for designing and interpreting studies that rely on vocal response to broadcasts of taped vocalizations to estimate owl populations (Forsman 1983, Pardieck et al. 1996) or investigate the behavioral contexts of particular vocalizations (Ritchison et al. 1988).

In 1997–98, I studied African Wood-Owls in Kibale National Park, Uganda to (1) describe the relationship between calling activity and season, lunar phase, cloud cover, and wind speed and (2) compare calling activity using three indices—whether or not owls were detected, number of individuals, and number of vocalizations.

STUDY AREA AND METHODS

Kibale National Park (KNP) covers 766 km² in western Uganda (0°13'–0°41'N, 30°19'–30°32'E). The topography is characterized by rolling hills and elevation ranges from 920 m above sea level in the south to 1590 m in the north. Yearly rainfall averages 1778 mm and there are two distinct rainy seasons each year (C. Chapman and L. Chapman unpubl. data; Fig. 1). About 58% of the park is covered by moist-evergreen forest, the remainder is secondary forest (19%), grassland (15%), swamp (4%), woodland (4%), and plantations (1%; Chapman and Lambert 2000). The forest is considered moist, evergreen forest, transitional between lowland rainforest and montane forest (Struhsaker 1997); common tree species include *Diospyros abyssinica*, *Markhamia platycalyx*, *Celtis durandii*, *Uvariopsis congensis*, and *Trilepsium phoberos* (Chapman et al. 1997). Canopy height ranges from 25–30 m, with a few trees as tall as 55 m.

I established two transects, one in the unlogged K-30 forestry compartment (282 ha) and the other in the K-14 (405 ha) and K-15 (347 ha) forestry compartments that were selectively logged in 1968 and 1969 (Struhsaker 1997). As a result of harvest and incidental damage, between 50% (K-15) and 25% (K-14) of all trees were destroyed in selectively-logged areas (Chapman et al. 2000)

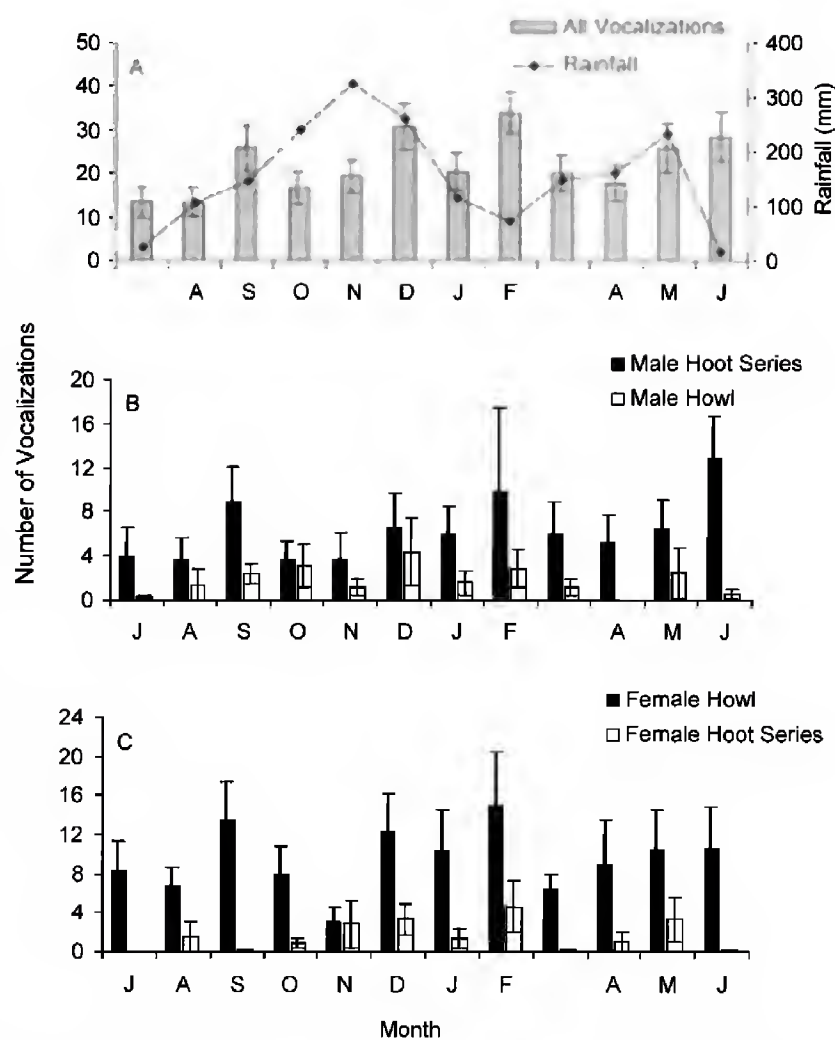


Figure 1. The mean (\pm SE) number of African Wood-Owl (*Strix woodfordii*) vocalizations detected per station ($N = 10$) per month between July 1997 and June 1998 and monthly rainfall recorded at Makerere University Biological Field Station, Kibale National Park, Uganda, for the same time period. Panel A is all vocalizations and monthly rainfall, panel B is male vocalizations only, and panel C is female vocalizations only.

and they now have a dense, brushy understory and a broken canopy when compared to unlogged areas (Chapman and Chapman 1997). Toward one end of both transects there was a short stretch (ca. 250–500 m) with pine plantation on one side of the transect and natural forest on the other.

Each transect had five survey points, located 0.5 km apart (total length = 2 km) along forest tracks that were used infrequently by motor vehicles and never at night when surveys were conducted. The spacing of these points was based on observations of African Wood-Owl densities in South Africa, where territories were located ca. 0.5 km apart along a 23 km stretch of riparian forest (Kemp and Kemp 1989). I surveyed transects from July 1997 through June 1998 generally beginning at 2000 H (ca. 1–1.5 hr after sunset) and finishing ca. 2 hr later. Logged and unlogged transects were sampled on an alternating schedule with one transect sampled per night. The end of the transect at which sampling was initiated was alternated between samples of the same transect. I surveyed transects four times a month, generally once a week, to distribute the sampling effort throughout the lunar cycle. I did not conduct surveys on nights with rain or high winds (ca. 15 kph).

At each point, I recorded five environmental variables. Forest was categorized as either logged or unlogged. Season was defined as either wet or dry, with the six wettest months (October–December, March–May) classified as wet season, and the six driest months (June–September, January–February) classified as dry season. Cloud cover was visually estimated and categorized as 0–25%, 25–50%, 50–75%, or 75–100%. Lunar phase was categorized into four periods centered on the first day of the new moon, first-quarter moon, full moon, and third-quarter moon. Wind speed was classified as one of three levels; no wind, light breeze (1–5 kph), and strong breeze (5–10 kph). After recording the environmental conditions, I recorded all vocalizations and the number of individuals detected during a 10-min listening survey. The number of individuals was a minimum number determined by distinguishing between male and female vocalizations, or, when more than one individual of the same gender was vocalizing, by recording the number of individuals heard calling simultaneously. I differentiated between four vocalization types described by Kemp and Kemp (1989): female hooting calls, female howls, male hooting calls, and male howls. Gender was determined by vocal pitch; female vocalizations are distinctly higher than males (Kemp and Kemp 1989). Single hoots and other vocalizations that did not fit these descriptions, or that could not be identified accurately to gender, were recorded under an “other calls” category.

I used generalized linear models (hereafter GLM; Crawley 1997, Seavy et al. in press) to evaluate if season, habitat, lunar phase, cloud cover, or wind speed were associated with the number of calls detected, number of owls detected, or whether or not an owl was detected (hereafter “presence/absence”). For presence/absence data I used a binomial distribution with a logit link and for the number of calls and number of owls detected I used negative binomial distributions with a log link. I began by considering each 10-min survey as an independent experimental unit. However, because the same stations were surveyed repeatedly during the course of the study, I also analyzed the data with generalized estimating equations (GEE) that adjusted for potential correlation among stations (Horton and Lipsitz 1999). I fit these models using independent, exchangeable, and autoregressive correlation structures and found that the results were not sensitive to the choice of correlation structure.

The GLMs are pseudoreplicated, increasing the risk of Type I error, but the small number of stations limits the power of the GEE approach, increasing the risk of Type II error. I have presented results of both analyses. However, recognizing the increased risk of type I error, I have cautiously discussed only the GLM results. All statistics were performed in SAS (version 9.0) using PROC GENMOD and results were considered significant if $P < 0.05$.

To present the results graphically, I calculated an expected value based on the total survey effort in each category of environmental conditions and then expressed the observed results as a percent deviation from expected.

RESULTS

African Wood-Owls were detected on 232 of 480 (48%) surveys. All detections were aural. Of the

Table 1. Association of seasonal, forest condition (logged or unlogged), weather, and lunar variables with calling activity of African Wood-Owls (*Strix woodfordii*) as measured by number of vocalizations detected, number of individuals detected, and the presence/absence of owls at survey stations. Comparisons made with generalized linear models, assuming each survey is independent, and generalized estimating equations using an exchangeable correlation structure that accounts for repeated measures of stations. Values in bold are statistically significant.

VARIABLE	GENERALIZED LINEAR MODEL CHI-SQUARE (P-VALUE)	GENERAL- IZED ESTIMATING EQUATION CHI-SQUARE (P-VALUE)
Number of vocalizations		
Wind speed	11.48 (<0.01)	7.99 (0.02)
Percent cloud cover	11.58 (<0.01)	6.56 (0.09)
Lunar phase	8.93 (0.03)	6.31 (0.10)
Forest: logged/unlogged	1.86 (0.17)	1.92 (0.17)
Season	0.94 (0.33)	0.93 (0.34)
Number of individuals		
Wind speed	7.90 (0.02)	4.60 (0.10)
Forest: logged/unlogged	1.82 (0.18)	1.41 (0.24)
Season	1.72 (0.19)	2.60 (0.11)
Lunar phase	3.55 (0.32)	3.70 (0.30)
Percent cloud cover	1.03 (0.79)	0.72 (0.87)
Presence/absence		
Lunar phase	7.61 (0.06)	4.80 (0.19)
Wind speed	4.89 (0.09)	3.02 (0.22)
Forest: logged/unlogged	1.41 (0.24)	0.83 (0.36)
Season	1.14 (0.29)	1.07 (0.30)
Percent cloud cover	2.13 (0.55)	1.89 (0.60)

232 surveys during which owls were heard, 56% were of a single owl, 35% were of two owls, and 9% were of 4–6 owls. I heard 2652 vocalizations; 29% were male hooting, 8% male howls, 7% female hooting, 43% female howls, and 13% other calls.

African Wood-Owls were consistently detected calling throughout the year; the greatest numbers of vocalizations were heard during the months of December and February, but there was not a pronounced seasonal pattern of calling activity (Fig. 1). There was no significant difference between wet and dry seasons for any of the response variables (Table 1). The mean number of vocalizations detected per station per month ranged from 13.3–

33.9 (Fig. 1). The absence of seasonal variation of calling activity was consistent for the different vocalizations given by males and females (Fig. 1). During surveys when I detected more than a single owl, males and females often called together in what have been described as “poorly synchronized duets” (Kemp 1987). These duets typically involved the one or two male hoot calls, answered by a female howl, and often continuing in this manner for 5-min or more. The African Wood-Owl was the only species detected; I never detected Red-chested Owlets (*Glaucidium tephronotum*) or Verreaux’s Eagle-Owls (*Bubo lacteus*), both of which occur in KNP (Skorupa 1983).

The statistical influence of environmental factors on calling activity varied depending on the index used and whether or not the model accommodated repeated measures (Table 1). For most response variables, the *P*-values for the association with environmental factors were greater when the GEE accounted for repeated measures (Table 1).

The number of vocalizations detected was the index most strongly influenced by environmental factors; the number of vocalizations differed among lunar phases, categories of cloud cover, and wind speeds (Table 1). Owls vocalized more often than expected during full moons and on clear nights, and less frequently during new moons and on cloudy nights (Fig. 2). Fewer calls were detected on nights with stronger winds (Fig. 2). These influences were much less pronounced when measured by the number of owls detected or by the presence/absence of owls (Fig. 2). When the number of individuals was analyzed, only wind speed was significant (Table 1). There was no influence of environmental factors as measured by the presence or absence of owls under different conditions. However, in both cases the nonsignificant trends were again consistent with differences at higher scales; I recorded fewer individuals and fewer detections during new moons and cloudy skies and more individuals and more detections during full moons and clear skies (Fig. 2). There was not a significant difference between the logged and unlogged transects for any of the response variables (Table 1).

DISCUSSION

The number of African Wood-Owl calls was correlated with lunar phase and cloud cover. Owls vocalized more during full moons and on clear nights, and less during new moons and on cloudy

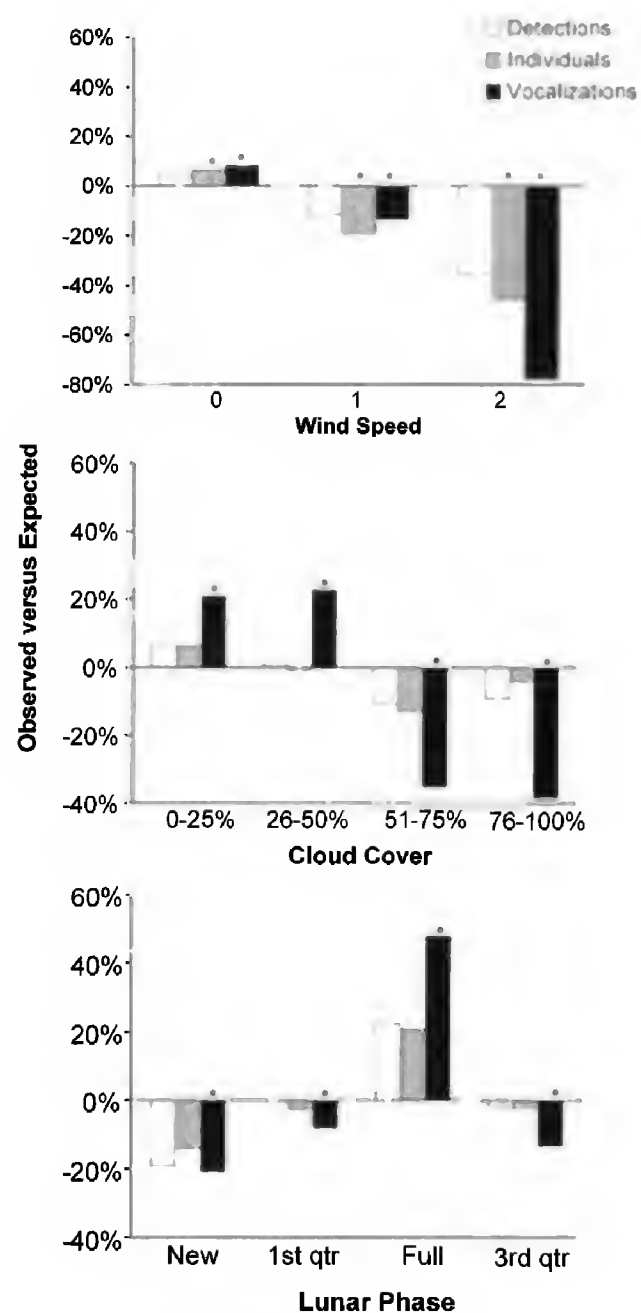


Figure 2. Percent difference between observed and expected [(obs – exp)/exp] number of African Wood-Owl (*Strix woodfordii*) vocalizations, individuals, and detections recorded during different wind speeds, cloud covers, and lunar phases at Kibale National Park, Uganda. * indicate environmental factors with significant relationships to response variables (statistics in Table 1).

nights. Although I did not detect a significant difference in the number of individuals nor in the number of detections, the direction of nonsignificant trends was consistent with the number of calls detected (Fig. 2).

In both temperate and tropical regions, owl calling activity is associated with lunar phase. When lunar phase is a significant factor, it is almost always due to more calling activity during brighter moon phases (Northern Saw-whet Owl [*Aegolius acadicus*], Clark and Anderson 1997; Great Horned Owl [*Bubo virginianus*], Morrell et al. 1991; Mottled Owl [*Ciccaba virgata*], Vermiculated Screech-Owl [*Megascops guatemalae*], Crested Owl [*Lophotrix crista-*

ta], Enriquez-Rocha and Rangel-Salazar 2001; and Elf Owl [*Micrathene whitneyi*], Hardy and Morrison 2000). This widespread pattern may result if increased activity (e.g., movement, hunting, and prey deliveries) on well-lit nights leads to a greater number of inter- and intra-pair vocal interactions.

Only Tawny Owls (*Strix aluco*; Hansen 1952) and Spotted Owls (*Strix occidentalis*; Ganey 1990) have been shown to respond negatively to moonlight, calling more on new moons than during brighter lunar phases. However, in not all cases is a positive association with moon phase consistent with a positive association with illumination. For example, of three tropical owls that increased calling activity during full moons, two decreased calling activity on bright nights (Enriquez-Rocha and Rangel-Salazar 2001). They explain these apparently contradictory results by noting that calling often occurred on dark nights with a full moon that was below the horizon or obscured by clouds. Predation risk, especially for small owls, may be a cost that reduces calling activity on moon-lit nights, but there is little evidence to either support or refute this hypothesis.

Calling activity of owls has been measured using a variety of sampling methods and indices of calling activity. This study demonstrated that the choice of index can affect the ability to identify environmental correlates of calling activity. I only detected significant effects of lunar phase and cloud cover based on the number of calls detected. Although calling activity was not significantly influenced when measured by number of individuals or presence/absence, in both cases nonsignificant trends were consistent with differences measured by the number of calls (Fig. 2). Studies that have measured presence/absence of owls may not have detected the influence of cloud cover and lunar phase that would be detected by measuring the number of vocalizations. Recording the number of owl vocalizations per survey may provide greater statistical power to detect relationships between calling activity and environmental factors. Designing studies that record multiple response variables may provide the most insight into these relationships.

African Wood-Owls called consistently throughout the year; I did not detect a difference in calling activity between rainy and dry seasons. In contrast, calling activity of many Nearctic and Palearctic owls that have been studied for an entire year usually show pronounced seasonal variation. Generally, vo-

cal activity of temperate owls peaks either late in the nesting season, when calls accompany frequent prey deliveries to nestlings (Lundberg 1980, but see Ganey 1990), or in late summer or early autumn when young are dispersing and adults may increase calling activity to defend territories (Ritchison et al. 1988, Lundberg 1980). In East Africa, African Wood-Owls have been recorded to lay eggs in January–March and August–November (Fry et al. 1988), suggesting a bimodal breeding season (laying–fledging) during January–April and August–December. However, there was no well-defined peak in calling activity timed within these periods (Fig. 1).

The number of vocalizations, the number of individuals, and the number of points where owls were detected were not significantly different between logged and unlogged areas. However, because the sample size in each habitat was limited ($N = 5$) and statistical power undoubtedly low, these data provide little information about the effects of logging on African Wood-Owl populations.

This study demonstrates that African Wood-Owls are highly vocal and that calling activity of this tropical owl is influenced by environmental factors. The vocal nature of African Wood-Owls, and their strong response to broadcasts of conspecific song (Kemp 1987), suggests that they could be effectively censused using standard playback techniques (Forsman 1983). The use of playbacks may provide such a strong behavioral stimulus that they mask environmental influences of spontaneous calling (Ganey 1990). However, when spontaneous calling is measured, the influence of environmental factors on calling activity should be considered when designing studies and interpreting results. The ability to measure the number of owls calling will be reduced on nights with even light wind (5–10 kph) and survey effort should be standardized to avoid lunar phase and cloud cover biases.

ACKNOWLEDGMENTS

Field assistance was provided by A. Randle and J. Paul. I thank L.J. Chapman, C.A. Chapman, and C.K. Apodaca for their support of this project. I express my gratitude to Makerere University Biological Field Station for providing logistical support in Kibale National Park. C.A. Chapman, J. Ganey, R. Gerhardt, J. Paul, D.W. Stahlecker, and an anonymous reviewer provided comments on earlier versions of this paper.

LITERATURE CITED

- CHAPMAN, C.A. AND L.J. CHAPMAN. 1997. Forest regeneration in logged and unlogged areas of Kibale National Park. *Biotropica* 29:396–412.

- , ———, R.W. WRANGHAM, G. ISABIRYE-BASUTA, AND K. BEN-DAVID. 1997. Spatial and temporal variability in the structure of a tropical forest. *Afr. J. Ecol.* 35:287–302.
- , S.R. BALCOMB, T.R. GILLESPIE, J.P. SKORUPA, AND T.T. STRUHSAKER. 2000. Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park. *Conserv. Biol.* 14:207–217.
- AND J.E. LAMBERT. 2000. Habitat alteration and the conservation of African primates: a case study of Kibale National Park, Uganda. *Am. J. Primatol.* 50:169–185.
- CLARK, K.A. AND S.H. ANDERSON. 1997. Temporal, climatic, and lunar factors affecting owl vocalizations of western Wyoming. *J. Raptor Res.* 31:358–363.
- CRAWLEY, M.J. 1997. GLIM for ecologists. Blackwell Science, Oxford, U.K.
- DELPORT, W., A.C. KEMP, AND J.W.H. FERGUSON. 2002. Vocal identification of individual African Wood-Owls *Strix woodfordii*: a technique to monitor long-term adult turnover and residency. *Ibis* 144:30–39.
- ENRIQUEZ-ROCHA, P.L. AND J.L. RANGEL-SALAZAR. 2001. Owl occurrence and calling behavior in a tropical rainforest. *J. Raptor Res.* 35:107–114.
- FORSMAN, E.D. 1983. Methods and materials for locating and studying Spotted Owls. U.S.D.A. For. Serv. Gen. Tech. Rep. PNW-GTR-162, Portland, OR U.S.A.
- FRY, C.H., S. KEITH, AND E.K. URBAN. 1988. The birds of Africa. Vol. 3. Princeton University Press, Princeton, NJ U.S.A.
- GANEY, J.L. 1990. Calling behavior of Spotted Owls in northern Arizona. *Condor* 92:485–490.
- GERHARDT, R.P. 1991. Response of Mottled Owls to broadcast of conspecific calls. *J. Field Ornithol.* 62:239–244.
- HANSEN, A.L. 1952. Natuglens (*Strix a. aluco*) dogn-og arsyrytyme. *Dan. Ornithol. Foren. Tidsskr.* 46:158–172.
- HARDY, P.C. AND M.L. MORRISON. 2000. Factors affecting the detection of Elf Owls and Western Screech Owls. *Wildl. Soc. Bull.* 28:333–342.
- HORTON, N.J. AND S.R. LIPSITZ. 1999. Review of software to fit generalized estimating equation regression models. *Am. Stat.* 53:160–169.
- KEMP, A.C. 1987. The owls of South Africa. Struik Winchester, Cape Town, South Africa.
- AND M.I. KEMP. 1989. The use of sonograms to estimate density and turnover of Wood-Owls in riparian forest. *Ostrich suppl.* 14:105–110.
- LUNDBERG, A. 1980. Vocalizations and courtship feeding of the Ural Owl *Strix uralensis*. *Ornis Scand.* 11:65–70.
- MARTIN, D.J. 1974. Copulatory and vocal behavior of a pair of Whiskered Owls. *Auk* 91:619–624.
- MORRELL, T.E., R.H. YAHNER, AND W.L. HARKNESS. 1991. Factors affecting detection of Great Horned Owls by using broadcast vocalizations. *Wildl. Soc. Bull.* 19:481–488.
- PARDIECK, K.L., J.M. MEYERS, AND M. PAGÁN. 1996. Surveys of Puerto Rican Screech-Owl populations in large-tract and fragmented forest habitats. *Wilson Bull.* 108:776–782.
- RITCHISON, G., P.M. CAVANAGH, J.R. BELTHOFF, AND E.J. SPARKS. 1988. The singing behavior of Eastern Screech-Owls: seasonal timing and response to playback of conspecific song. *Condor* 90:648–652.
- SEAVY, N.E., S. QUADER, J.D. ALEXANDER, AND C.J. RALPH. In press. Generalized linear models and point count data: statistical considerations for the design and analysis of monitoring studies. In C.J. Ralph and T.D. Rich [Eds.], Bird conservation implementation and integration in the Americas. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-191, Arcata, CA U.S.A.
- SKORUPA, J.P. 1983. Kibale Forest bird checklist. *NY Zool Soc. Publ.* 1–11.
- STEYN, P. AND J. SCOTT. 1973. Notes on the breeding biology of the Wood-Owl. *Ostrich* 44:118–125.
- STRUHSAKER, T.T. 1997. Ecology of an African rain forest logging in Kibale and the conflict between conservation and exploitation. Univ. Press Florida, Gainesville, FL U.S.A.

Received 15 September 2003; accepted 25 May 2004

Associate Editor: Ian G. Warkentin

DIETS AND FORAGING BEHAVIOR OF NORTHERN SPOTTED OWLS IN OREGON

ERIC D. FORSMAN¹

U.S. Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331 U.S.A.

ROBERT G. ANTHONY AND E. CHARLES MESLOW²

USDI Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331 U.S.A.

CYNTHIA J. ZABEL

U.S. Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, CA 95521 U.S.A

ABSTRACT.—We describe local, regional, and annual variation in diets of northern Spotted Owls (*Strix occidentalis caurina*) in Oregon based on 24 497 prey collected at 1118 owl territories in 1970–2003. The sample included 91.5% mammals, 4.3% birds, 4.1% insects, and 0.1% other prey. The diet included ≥ 131 species, including 49 mammals, 41 birds, 3 reptiles, 1 frog, 1 crayfish, 1 scorpion, 2 snails, and 33 species of insects. On average, $91.9 \pm 0.3\%$ (SE) of prey in the diet were nocturnal animals, $3.3 \pm 0.2\%$ were diurnal, and $4.8 \pm 0.2\%$ were active both day and night. Of the prey captured, $50.5 \pm 0.8\%$ were arboreal, $18.7 \pm 0.7\%$ were scansorial, $4.8 \pm 0.2\%$ were aerial, and $26.0 \pm 0.7\%$ were terrestrial. Mean mass of prey was 116.6 ± 6.5 g. Diets varied among owl territories, geographic regions, and years; but were generally dominated by four to six species of nocturnal mammals, including northern flying squirrels (*Glaucomys sabrinus*), woodrats (*Neotoma fuscipes* and *N. cinerea*), red tree voles (*Arborimus longicaudus*), western red-backed voles (*Clethrionomys californicus*), deer mice (*Peromyscus maniculatus*), or gophers (*Thomomys* spp.). Estimates of dietary evenness were low, indicating diets dominated by a few species of mammals. Forest management practices that produce healthy populations of arboreal and scansorial mammals such as flying squirrels, woodrats, and red tree voles should benefit northern Spotted Owls in Oregon and Washington.

KEY WORDS: *northern Spotted Owl*; *Strix occidentalis caurina*; *diet*; *prey selection*; *northern flying squirrel*; *Glaucomys sabrinus*; *red tree vole*; *Arborimus longicaudus*.

DIETA Y COMPORTAMIENTO DE FORRAJE O DE *STRIX OCCIDENTALIS CAURINA* EN OREGON

RESUMEN.—Describimos la variación local, regional y anual en la dieta de *Strix occidentalis caurina* en Oregon en base a 24 497 presas colectadas en 1118 territorios de los buhos para el reñudo 1970–2003. La muestra incluyó 91.5% de mamíferos, 4.3% de aves, 4.1% de insectos y 0.1% de otras presas. La dieta incluyó ≥ 131 especies, incluyendo 49 mamíferos, 41 aves, 3 reptiles, 1 rana, 1 pez, 1 escorpión, 2 caracoles y 33 especies de insectos. En promedio $91.9 \pm 0.3\%$ (SE) de las presas en la dieta fueron animales nocturnos, $3.3 \pm 0.2\%$ fueron diurnos y $4.8 \pm 0.2\%$ fueron activos durante el día y la noche. De las presas capturadas, $50.5 \pm 0.8\%$ fueron arboreas, $18.7 \pm 0.7\%$ fueron scansorial, $4.8 \pm 0.2\%$ fueron aéreas y $26.0 \pm 0.7\%$ fueron terrestres. La media de la masa de las presas fue de 116.6 ± 6.5 gm. Las dietas variaron entre los territorios de los buhos, las regiones geográficas y los años; pero fueron generalmente dominadas entre cuatro a seis especies de mamíferos nocturnos, incluyendo a ardillas voladoras (*Glaucomys sabrinus*), ratas (*Neotoma fuscipes* y *N. cinerea*) y ratones (*Arborimus longicaudus*, *Clethrionomys californicus*, *Peromyscus maniculatus*, y *Thomomys* spp.). Las estimaciones de la uniformidad de la dieta fueron bajas, indicando que la dieta fue dominada por unas pocas especies de mamíferos. Las prácticas forestales que producen poblaciones saludables de mamíferos como ardillas voladoras, ratas y ratones deben favorecer a los buhos en Oregon y Washington.

[Traducción de César Márquez]

¹ E-mail address: eforsman@fs.fed.us

² Present address: 8035 NW Oxbow, OR 97330 U.S.A.

Home-range areas, population cycles, and behavior of owls are greatly influenced by the distribution, density, and behavior of their prey. To understand these relationships, biologists need detailed information on the diet of the predator, including data on local and regional variation. Examination of the diet can provide many clues regarding foraging behavior, habitat selection, and degree of dietary specialization. This information is particularly important for understanding which types of prey are most important to a predator in different regions, and for understanding the numeric impact of the predator on its prey.

There have been numerous studies of northern Spotted Owls (*Strix occidentalis caurina*) in Oregon, Washington, and California. The earliest of these studies focused primarily on distribution, basic life history attributes, dispersal, and habitat selection of the species (e.g., Gould 1977, Barrows 1980, Forsman et al. 1984, Miller 1989, Carey et al. 1992, Miller et al. 1997, Zabel et al. 1995, Thraillkill et al. 1997). These pioneering efforts have been followed by nearly 20 yr of demographic studies, in which researchers used mark-recapture methods to estimate population trends of the owl (e.g., Burnham et al. 1994, Forsman et al. 1996, Franklin et al. 2000). During many of these studies, investigators routinely collected pellets from Spotted Owl roost areas to determine the composition of the diet. Some of these data have been published (e.g., Forsman et al. 1984, Barrows 1980, Thomas et al. 1990, Ward 1990, Zabel et al. 1995), but most of the data from Oregon have never been published. In 1996–2003, we contacted most of the researchers who have studied Spotted Owls in Oregon and solicited their assistance in compiling all of the available information on the diet of the Spotted Owl in Oregon. Here, we summarize results of that effort, compare regional, local, and annual variation in the diet; and estimate annual number of prey captured by individual Spotted Owls in different regions.

STUDY AREA

The study area included western Oregon and the eastern slopes of the Cascades Range (Fig. 1). With the exception of the lowland interior valleys of western Oregon, this region is characterized by mountainous terrain covered by coniferous forests. Forest composition is predominantly Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) in the Coast Ranges and western Cascades Range, mixed-conifer or mixed-evergreen forests in southern Oregon, and mixed conifer forests on the east slope of the Cascades (Franklin and Dyr-

ness 1973). For our analysis we subdivided the study area into seven geographic regions (Fig. 1). Regional boundaries followed county lines, except that we used Interstate Highway 5 to subdivide samples from the Coast and Cascades ranges (Fig. 1). The eastern edge of the study area corresponded with the eastern limits of the range of the Spotted Owl in Oregon (Fig. 1).

METHODS

Pellets were collected below owl roosts, air-dried, and stored in labeled plastic bags until they could be analyzed. Some pellets were obtained from radio-marked owls during fall and winter (Forsman et al. 1984, Miller et al. 1997), but most were collected during the breeding season (March–August) when we visited historic nest areas to locate and band owls. With the exception of a few radio-marked owls (Forsman et al. 1984), no attempt was made to sample different individuals or territories randomly or systematically, although many territories were sampled in multiple years. Territories were identified based on occupancy by pairs of Spotted Owls, many of which were banded or radio-marked.

We based all analyses on the estimated number of prey or biomass of prey in each sample. We estimated the number of prey in each sample by counting skulls, mandibles, bones of the appendicular skeleton, or pieces of exoskeleton, whichever gave the highest count. In a few cases we also used hair or feathers to identify prey. To avoid double counting remains of large prey that appeared in several pellets, we combined remains from multiple pellets or pellet fragments found at the same roost on the same date. We used dichotomous keys (Maser and Storm 1970, Verts and Carraway 1984) and a reference collection of bird and mammal skeletons to identify remains in pellets.

We estimated biomass by multiplying the number of individuals of each species in a sample by the mean mass of the species, or by estimating and summing the unique mass of each prey item in the sample. The latter method was used only for large prey such as snowshoe hare (*Lepus americanus*), brush rabbits (*Sylvilagus bachmani*), and mountain beaver (*Aplodontia rufa*), because those prey types were mostly represented in our samples by small juveniles, and would have been overestimated if we used mean mass from museum specimens. For these species, we estimated mass based on comparisons of bones with specimens of known mass in our reference collection and we made the simplifying assumption that mass was linearly correlated with the size of bones in pellets. Estimates of mean mass for birds and mammals were obtained from Dunning (1993) and Verts and Carraway (1998; Appendix). For invertebrates, snakes, lizards, and amphibians, we used estimates of mean mass from local specimens or from similar species in the published literature (Smith and Murphy 1973; Appendix).

To evaluate when and where owls were foraging, we subdivided prey into groups based on their primary period of activity (nocturnal, diurnal, or both), and their primary activity zone (terrestrial, arboreal, scansorial, or aerial; Appendix). These classifications were based on information in Verts and Carraway (1998) as well as our own observations of animals in our study areas. For this analysis we classified mammals as arboreal if they nested

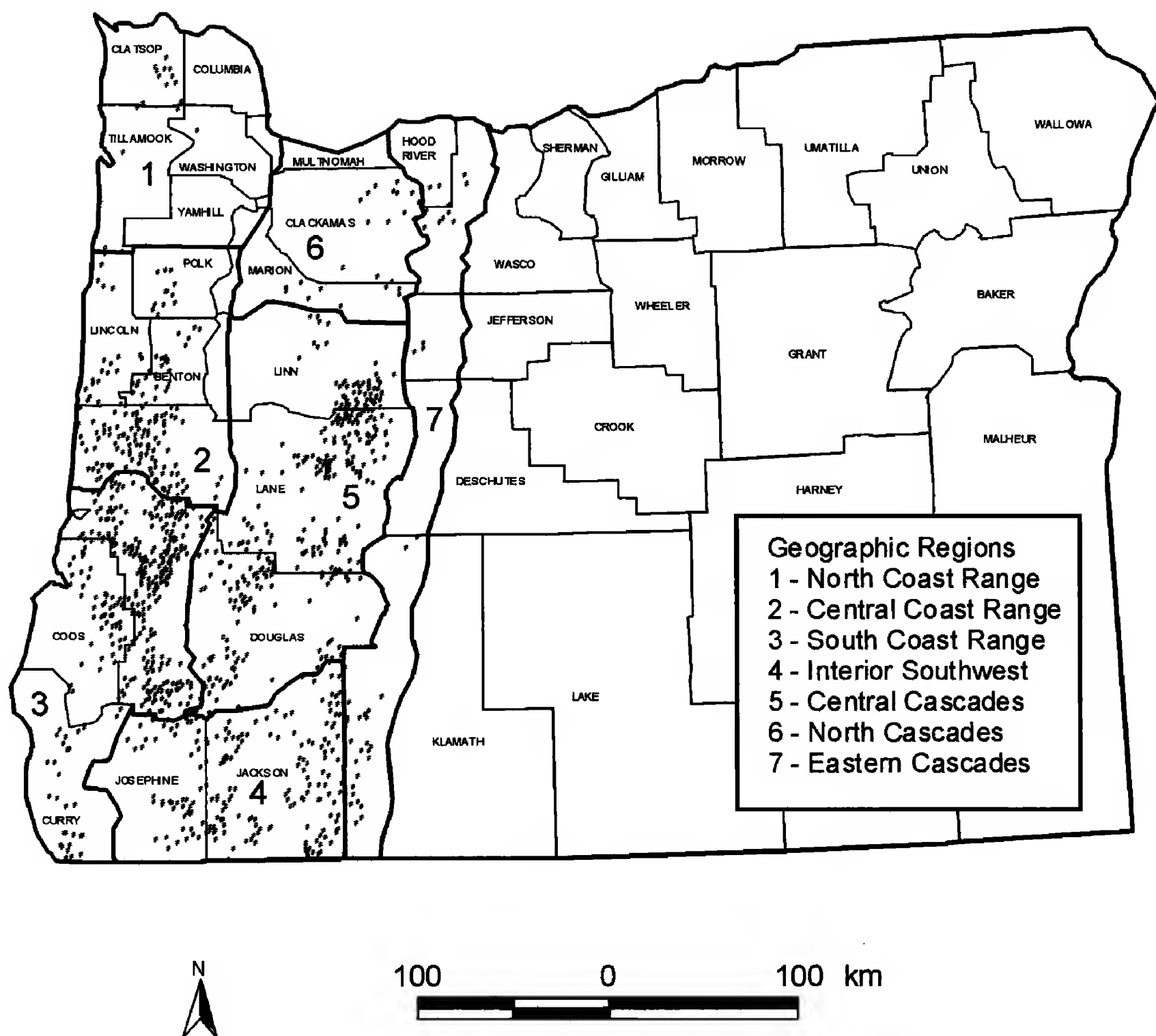


Figure 1. The Oregon study area, illustrating locations of 1118 northern Spotted Owl territories from which we collected data on owl diets, and seven geographic regions that we used for regional comparisons of diet. Boundaries of geographic regions followed county lines except that we used Interstate Highway 5 to divide samples from the Coast Ranges and Cascades Mountains north of Josephine County (solid dark line bisecting Douglas, Lane, Linn, Marion, Clackamas, and Multnomah counties).

primarily in trees, and scansorial if they spent much of their time climbing in trees but often nested on the ground (Appendix). This analysis provided a general measure of the amount of owl foraging that occurred in different time periods or activity zones, as we knew from field observations that prey were not always captured in their primary activity periods or activity zones (Sovern et al. 1994).

We used all prey remains to compile a list of species captured by northern Spotted Owls (Appendix). We estimated mean dietary composition by computing the diet in each owl territory, and averaging across territories to get the mean and SE for each prey category. Estimates

of means were based on a subset of owl territories from which we obtained samples of ≥ 10 prey items, regardless of the number of years in which pellets were collected at a particular territory. We selected 10 as the minimum sample size for analysis after exploratory analyses with larger sample sizes (i.e., 20, 50) indicated that the choice of minimum sample size made little difference to our conclusions. We estimated mean mass of prey captured by each pair of owls by dividing the total biomass in the sample by the number of prey in the sample. Regional means were then estimated by averaging among pairs.

For comparisons of dietary composition among and within regions we subdivided the diet into 18 prey cate-

gories and used one-way analysis of variance to compare mean proportions of each prey type in the diet. Statistical tests of proportional data were based on arcsine transformations to better meet the assumptions of the tests (Sokal and Rohlf 1969). However, the results were virtually identical regardless of whether the data were transformed or not, so we present the untransformed data in all tables and figures.

To compare the evenness of the diet in different regions we used the reciprocal of Simpson's Index (Hill 1973). Simpson's Index (q) is equal to the sum of the squared values of the proportional abundances of all species (or groups) in a sample (Hill 1973). For a given sample, the range of q is from $1/N$ (all species equally abundant) to 1 (only one species in diet). Conversely, the reciprocal of Simpson's Index ($1/q$) ranges from $1-N$, where 1 indicates a diet composed entirely of one species, and N is a diet composed of more than one species with all species equally represented in the diet. In our case, minimum and maximum values of $1/q$ were 1 and 18, where 1 indicated a diet composed entirely of 1 species, and 18 indicated a diet in which all 18 prey groups were equally represented. We estimated the mean $1/q$ for each region as $(\sum^N 1/q)/N$, where N = the number of territories in the sample.

We used χ^2 tests to examine among-year variation in the diet at individual territories that had samples of ≥ 20 prey in 2 or more years. For this analysis we lumped prey into seven groups: (1) Lagomorphs (*Lepus americanus*, *Sylvilagus bachmani*), (2) northern flying squirrels (*Glaucomys sabrinus*), (3) deer mice (*Peromyscus maniculatus*), (4) woodrats (*Neotoma fuscipes*, *N. cinerea*), (5) western red-backed voles (*Clethrionomys californicus*), (6) red tree voles (*Arborimus longicaudus*), and (7) all other prey.

We used linear regression to examine relationships between elevation and the numeric proportion of several species of small mammals in the diet. For this analysis we used a single estimate of the overall diet at each territory, regardless of when pellets were collected, and we used a single estimate of elevation at each owl territory, based on the elevation at the nest site or primary roost area. We determined elevations with altimeters, topographic maps, or a 30-m-resolution digital elevation map.

We estimated the number of prey captured per year by individual owls based on the assumption that a Spotted Owl of average mass (610 g) consumes 12% of its body mass (73.2 g) of food per day, or 26 718 g/yr. The number of each species captured per year was then estimated by multiplying the proportional biomass of each species in the diet by 26 718 and dividing by the mean mass of the species. The critical assumption in this analysis was the amount of food consumed per day. We could have used a more conservative estimate of 56–59 g/d (Weathers et al. 2001), but we chose to use a slightly higher estimate because we wanted to allow for the fact that Spotted Owls often discard stomachs, intestines, tails, and other parts of the prey that they capture. Thus, we felt that our estimate of 12% of body mass was a reasonable measure of the amount of prey captured per day, especially considering other data on food consumption of Spotted Owls (Forsman 1980) and other owls (Graber 1962). To estimate the number of prey captured per year in each owl territory we multiplied the number of prey

captured per owl by 2.0 for non-nesting pairs, and 2.6 for nesting pairs with two young. Estimates of prey capture for adults with young assumed that nesting pairs fed their young for ca. 4 mo (Forsman et al. 1984), and that the mean biomass consumed per day was the same for juveniles and adults. The latter assumption was a simplification of the actual rate of daily food intake by juveniles, which was small at first, and then increased as juveniles matured.

All statistical analyses were conducted with Program SPSS (Version 11.5, SPSS Inc., Chicago, IL U.S.A.). We set the significance level for statistical tests at $\alpha = 0.05$. All means are expressed as $\bar{x} \pm 1$ SE.

RESULTS

Attributes of Prey. We identified 24 497 prey items from 1118 owl territories, including 547 territories with $N > 10$ (Fig. 1). The total sample included 91.5% mammals, 4.3% birds, 4.1% insects, and 0.1% other prey (Appendix). The sample included at least 131 species; 49 mammals, 41 birds, 3 reptiles, 1 frog, 1 crayfish, 1 scorpion, 2 snails, and 33 insects (Appendix). On average, $91.9 \pm 0.3\%$ of prey in the diet were nocturnal animals, $4.8 \pm 0.2\%$ were active both day and night, and $3.3 \pm 0.2\%$ were diurnal ($N = 547$). Of the prey captured, $50.5 \pm 0.8\%$ were arboreal, $26.0 \pm 0.7\%$ were terrestrial, $18.7 \pm 0.7\%$ were scansorial, and $4.8 \pm 0.2\%$ were aerial ($N = 547$). The percent of prey that were either arboreal or scansorial was 70.8% in the North Coast, 74.8% in the Central Coast, 77.8% in the South Coast, 64.8% in the Interior Southwest, 59.2% in the Central Cascades, 56.7% in the North Cascades, and 64.3% in the East Cascades. Mean mass of prey ranged from 91–142 g in the seven regions, and was 116.6 ± 6.5 g overall (Table 1).

Dietary Evenness. Mean estimates of dietary evenness ($1/q$) for all regions were near the lower end of the scale of possible values, indicating diets dominated by a few species in all regions (Table 2). Diets were most even in the Central Cascades, Interior Southwest, South Coast, and Eastern Cascades regions, and least even in the North Cascades, North Coast, and Central Coast regions (Table 2).

Regional Differences in Diet. Composition of the diet differed among regions for 16 of the 18 prey categories in Table 2 (P -values < 0.05). The only two categories that did not differ among regions were the "Bats" category ($P = 0.70$) and the category "Other," which included miscellaneous prey such as molluscs, snakes, lizards, and scorpions ($P = 0.21$). In some cases, differences among

Table 1. Mean mass (g) of prey captured by northern Spotted Owls in different regions of Oregon, 1970–2003. *N* is the number of owl territories sampled in each region.

REGION	<i>N</i>	MEAN ± SE	RANGE	95% CI
North Coast Region	9	123.6 ± 10.3	75–173	100–147
Central Coast Region	90	112.8 ± 3.2	41–213	106–119
Southern Coast Region	180	131.4 ± 2.7	55–317	126–137
Interior Southwest	75	142.1 ± 5.0	25–242	132–152
Central Cascades	154	108.5 ± 2.7	44–209	103–114
North Cascades	4	90.7 ± 14.1	67–130	46–136
East Cascades	35	106.7 ± 7.3	11–247	92–121
All areas ¹	7	116.6 ± 6.5		

¹ Grand mean of seven regional means.

regions were expected because some prey species, such as American pikas (*Ochotona princeps*) and red tree voles did not occur in all regions. In most cases, however, there were no obvious *a priori* reasons to expect regional variation in prey composition.

Although there was considerable variation among regions, the diet in all areas was composed mainly of four to six species of nocturnal mam-

mals, including northern flying squirrels, woodrats, red tree voles, western red-backed voles, deer mice, or gophers (*Thomomys* spp.; Tables 2–3). Northern flying squirrels were the most common animal in the diet in most regions, averaging 28–52% of prey numbers and 30–74% of prey biomass (Tables 2–3). Woodrats comprised $11.7 \pm 3.3\%$ of prey numbers, $24.9 \pm 5.3\%$ of prey biomass, and were most

Table 2. Mean percent (±1 SE) of prey numbers in diets of northern Spotted Owls in seven different geographic regions of Oregon, 1970–2003. Sample size (number of owl territories with ≥10 prey items) is in parentheses. “T” indicates trace amount (<0.05%).

PREY ^a	NORTH COAST (9)	CENTRAL COAST (90)	SOUTH COAST (180)	INTERIOR SOUTHWEST (75)	CENTRAL CASCADES (154)	NORTH CASCADES (4)	EASTERN CASCADES (35)
Shrews	1.8 ± 1.4	0.9 ± 0.2	1.2 ± 0.2	2.8 ± 0.6	1.9 ± 0.3	2.5 ± 2.5	1.5 ± 0.5
Moles		0.2 ± 0.1	0.1 ± 0.0	2.8 ± 0.6	1.0 ± 0.2		1.2 ± 0.5
Bats		0.2 ± 0.1	0.5 ± 0.1	0.3 ± 0.2	0.4 ± 0.1		0.3 ± 0.2
Rabbits/hares	0.8 ± 0.4	3.6 ± 0.5	4.6 ± 0.4	2.6 ± 0.4	4.8 ± 0.4		4.5 ± 0.8
American pika				0.1 ± 0.1	0.9 ± 0.2		0.3 ± 0.2
Douglas’ squirrel	1.3 ± 0.8	0.6 ± 0.2	0.3 ± 0.1	0.1 ± 0.1	0.4 ± 0.1		0.1 ± 0.1
Chipmunks	2.1 ± 1.4	0.7 ± 0.2	0.6 ± 0.1	1.5 ± 0.3	1.4 ± 0.2	2.3 ± 2.3	1.3 ± 0.5
N flying squirrel	48.3 ± 3.6	49.5 ± 1.6	36.0 ± 1.2	28.2 ± 2.0	34.6 ± 1.2	52.1 ± 8.7	38.9 ± 3.1
Gophers	2.6 ± 1.3	0.6 ± 0.2	0.1 ± 0.1	5.4 ± 0.9	4.9 ± 0.6		6.5 ± 1.7
Deer mouse	17.3 ± 5.4	10.5 ± 1.1	6.2 ± 0.6	4.9 ± 0.6	6.1 ± 0.7		2.9 ± 0.7
Woodrats	11.1 ± 2.8	7.1 ± 0.8	18.2 ± 0.9	27.8 ± 2.4	9.5 ± 1.0	2.3 ± 2.3	8.2 ± 1.8
W red-backed vole		2.2 ± 0.4	2.8 ± 0.3	6.8 ± 0.7	11.0 ± 0.7	26.9 ± 8.7	10.4 ± 1.6
Red tree vole	4.8 ± 2.7	12.7 ± 1.1	18.2 ± 0.9	2.6 ± 0.7	7.7 ± 0.8		
<i>Microtus</i> spp.		1.2 ± 0.3	1.5 ± 0.2	2.5 ± 0.5	2.6 ± 0.4		1.1 ± 0.3
Other mammals	3.8 ± 1.8	3.9 ± 0.5	3.7 ± 0.3	1.4 ± 0.3	5.1 ± 0.4		3.9 ± 0.8
Birds	3.8 ± 1.2	3.9 ± 0.4	3.6 ± 0.3	5.7 ± 0.9	4.1 ± 0.3	13.9 ± 6.1	4.3 ± 0.8
Insects	1.0 ± 0.6	2.1 ± 0.7	2.4 ± 0.3	4.3 ± 1.2	3.5 ± 0.6		14.5 ± 3.1
Other	0.4 ± 0.4	0.1 ± 0.0	T	0.1 ± 0.1	0.1 ± 0.1		0.1 ± 0.1
Sum (%)	100.0	100.0	100.0	100.0	100.0	100.0	100.0
1/ <i>q</i> ^b	3.1 ± 0.2	3.2 ± 0.1	3.9 ± 0.1	3.9 ± 0.2	4.5 ± 0.1	2.4 ± 0.2	3.7 ± 0.3

^a See appendix for complete list of common and scientific names of prey.

^b 1/*q* = reciprocal of Simpson’s Index.

Table 3. Mean percent (± 1 SE) of prey biomass in diets of northern Spotted Owls in seven different geographic regions of Oregon, 1970–2003. Sample size (number of owl territories with ≥ 10 prey items) is in parentheses. “T” indicates trace amount ($<0.05\%$).

PREY ^a	NORTH COAST (9)	CENTRAL COAST (90)	SOUTH COAST (180)	INTERIOR SOUTHWEST (75)	CENTRAL CASCADES (154)	NORTH CASCADES (4)	EASTERN CASCADES (35)
Shrews	0.1 \pm 0.1	0.1 \pm T	0.1 \pm T	0.1 \pm 0.1	0.1 \pm T	0.2 \pm 0.2	0.1 \pm 0.1
Moles		0.1 \pm T	T	1.3 \pm 0.3	0.6 \pm 0.1		0.7 \pm 0.3
Bats		T	T	T	T		T
Rabbits/hares	2.2 \pm 1.1	9.9 \pm 1.3	11.6 \pm 1.0	5.9 \pm 1.1	12.9 \pm 1.1		12.3 \pm 2.6
American pika				0.1 \pm 0.1	1.4 \pm 0.3		0.5 \pm 0.3
Douglas’ squirrel	1.9 \pm 1.1	1.2 \pm 0.3	0.5 \pm 0.1	0.3 \pm 0.2	0.7 \pm 0.2		0.3 \pm 0.2
Chipmunks	1.7 \pm 1.1	0.5 \pm 0.1	0.4 \pm 0.1	1.2 \pm 0.2	1.2 \pm 0.2	1.4 \pm 1.4	1.2 \pm 0.5
N. flying squirrel	52.3 \pm 3.9	58.3 \pm 1.6	38.6 \pm 1.6	30.2 \pm 2.5	45.5 \pm 1.7	74.5 \pm 4.5	50.7 \pm 4.2
Gophers	2.5 \pm 1.3	0.5 \pm 0.2	0.1 \pm T	4.3 \pm 0.7	4.8 \pm 0.6		7.5 \pm 2.3
Deer mouse	3.8 \pm 1.5	2.5 \pm 0.3	1.2 \pm 0.1	1.0 \pm 0.1	1.4 \pm 0.2		0.7 \pm 0.2
Woodrats	25.8 \pm 4.7	16.1 \pm 1.5	37.1 \pm 1.6	48.5 \pm 3.4	20.7 \pm 1.8	5.0 \pm 5.0	18.2 \pm 3.4
W. red-backed vole		0.5 \pm 0.1	0.6 \pm 0.1	1.3 \pm 0.2	2.7 \pm 0.2	8.2 \pm 3.3	2.8 \pm 0.6
Red tree vole	1.0 \pm 0.6	3.7 \pm 0.5	4.2 \pm 0.3	0.6 \pm 0.2	2.2 \pm 0.3		
<i>Microtus</i> spp.		0.3 \pm 0.1	0.4 \pm 0.1	0.6 \pm 0.1	0.9 \pm 0.1		0.4 \pm 0.1
Other mammals	4.2 \pm 2.4	2.4 \pm 0.4	2.4 \pm 0.3	0.9 \pm 0.4	1.9 \pm 0.2		1.0 \pm 0.3
Birds	4.3 \pm 2.3	3.9 \pm 0.5	2.8 \pm 0.3	3.5 \pm 0.6	2.8 \pm 0.3	10.7 \pm 5.9	2.9 \pm 0.9
Insects	T	T	T	0.1 \pm 0.1	0.1 \pm T		0.7 \pm 0.4
Other	0.1 \pm 0.1	T	T	T	T		T
Sum (%)	100.0	100.0	100.0	100.0	100.0	100.0	100.0

^a See appendix for complete list of common and scientific names of prey.

important in the diet in the Interior Southwest and South Coast regions (Tables 2–3). Red tree voles comprised $6.6 \pm 2.6\%$ of prey numbers, and were most common in the diet in the South and Central Coast regions (Tables 2–3). Western red-backed voles were uncommon in the diet in all coastal regions, but comprised 7–27% of prey numbers in the Cascades and Interior Southwest regions (Table 2). Deer mice comprised $6.8 \pm 2.1\%$ of prey numbers, with the highest occurrence in the Central and Northern Coast ranges (Table 2). Gophers comprised 5–6% of prey numbers in the Interior Southwest, Central Cascades and Eastern Cascades regions, but were comparatively rare or uncommon in the diet in all coastal regions (Table 2). Chipmunks (*Tamias* spp.) and Douglas’ squirrels (*Tamiasciurus douglasii*) together comprised 1–3% of prey numbers.

Brush rabbits and/or snowshoe hare comprised 1–5% of the prey captured and 2–13% of the biomass in the diet (Tables 2–3). Of 1010 rabbits or hares found in pellets, 826 (81.8%) were juveniles, 63 (6.2%) were subadults, 114 (11.3%) were adults, and 7 (0.7%) were of undetermined age. The estimated mean mass of individual rabbits and

hares in pellets was 340 ± 6 g (range = 50–1400 g). American pikas occurred only in the Cascades and Interior Southwest regions, where they averaged less than 1% of prey numbers (Table 2).

Bats (Chiroptera), shrews (*Sorex* spp.), and moles (*Scapanus* spp.) were uncommon in the diet in all areas except the Interior Southwest Region, where the average diet included 5.6% shrews and moles (Table 2). The category “Other mammals” in Tables 2–3 included small mammals that we could not identify to species as well as a variety of small and medium-sized mammals that were uncommon in the diet. These included weasels (*Mustela erminea*, *M. frenata*), heather voles (*Phenacomys intermedius*), white-footed voles (*Arborimus albipes*), mountain beaver, western gray squirrels (*Sciurus griseus*), ground squirrels (*Spermophilus beecheyi*, *S. lateralis*), spotted skunks (*Spilogale gracilis*), ringtails (*Bassariscus astutus*), and jumping mice (*Zapus trinotatus*, *Z. princeps*; Appendix).

Of 56 mountain beaver in pellets, 55 were juveniles, 1 was a small subadult, and 48 (85%) were captured in June or early July, when juvenile mountain beaver first began to emerge from their natal dens (Lovejoy 1972). The five ringtails found in

pellets were all small juveniles with estimated mass = 200–400 g. The only spotted skunk was a sub-adult, with estimated mass ca. 500 g.

Birds averaged $5.6 \pm 1.4\%$ of prey numbers and $4.4 \pm 1.1\%$ of prey biomass (Tables 2–3). Most small or medium-size birds that occurred in the forests of western Oregon were taken at least occasionally (Appendix). Of 540 birds identified to species or family, the most common were jays (17.6%), small owls (23.0%), woodpeckers (12.8%), grouse and quail (3.7%), and Varied Thrushes (*Ixoreus naevius*) or American Robins (*Turdus migratorius*) (24.4%). In most cases we could not differentiate between skeletons of Varied Thrushes and American Robins, so we combined them for analysis.

Insects were generally uncommon in the diet, except in the Eastern Cascades Region (Table 2). Of 1005 insects identified, the two most common species were the great grig (*Cyphoderris monstrosa*), a large scansional cricket (41.0%), and the ponderous borer (*Ergates spiculatus*), a large wood-boring beetle (24.8%). Great grigs occurred only in the Cascades Range, where we commonly heard them on summer nights, as they stridulated from elevated perches on tree trunks or tree limbs. Adult ponderous borers were noisy, clumsy fliers that frequently crashed into limbs while flying through the forest at night.

Other items in the diet included frogs (*Rana* spp.), snakes (*Thamnophis ordinoides*, *T. spp.*), lizards (*Sceloporus occidentalis*, *Elgaria coeruleus*), terrestrial snails (*Haplotrema vancouverense*, *Monedenia fidelis*), crayfish (*Pacifastacus leniusculus*), and scorpions (*Uroctonus mordax*). All of these were rare in the diet (<0.1% of total prey; Appendix).

Local and Annual Variation in Diet. Composition of the diet was highly variable among owl territories within regions (all P -values <0.05). While some of this variation was probably the result of small sample size, we found similar results even when we limited the analysis to territories with samples >50 (data not presented). This suggested that dietary variation among territories was due to factors other than sample size.

Composition of the diet varied among years ($P < 0.05$) at 25 of 56 territories where we collected ≥ 20 prey in 2 or more years. In most cases, the differences were relatively small, but there were notable exceptions. For example, at two territories the percent of tree voles and flying squirrels in the diet varied dramatically among years (Table 4). At

Table 4. Annual variation in diet at two different northern Spotted Owl territories in Oregon. Numbers indicate percent of total prey in each annual sample. Annual sample sizes are in parentheses.

SPECIES/GROUP	OAK CREEK				Brummet	
	1970 (174)	1972 (89)	1973 (34)	1974 (95)	1990 (45)	1991 (47)
Rabbits/hares	1	2		2		2
N. flying squirrel	5	37	29	6	47	15
Deer mouse	8	15		79	5	8
Woodrats	2	8	3		13	9
W. red-backed vole		3				
Red tree vole	66	10	44	11	33	60
Other prey	18	25	24	2	2	6
Total %	100	100	100	100	100	100

the Oak Creek territory, deer mice varied from 0% of the diet in one year to 79% of the diet in another year (Table 4).

Variation in Diet with Changing Elevation. In the Cascades Mountains (Central Cascades, North Cascades, East Cascades regions), predation on red-backed voles and gophers was positively correlated with elevation (red-backed vole $F_{1,191} = 27.7$, $P < 0.001$, $R^2 = 0.127$; gophers $F_{1,191} = 17.66$, $P < 0.001$, $R^2 = 0.085$). In the Central Cascades Region, predation on red tree voles was negatively correlated with elevation ($F_{1,152} = 32.6$, $P < 0.001$, $R^2 = 0.177$). Further examination of the data from the Central Cascades Region revealed that tree voles comprised only $2.3 \pm 0.6\%$ of the diet at territories above 975 m elevation ($N = 51$), compared to $10.3 \pm 1.1\%$ of the diet at territories below 975 m ($N = 103$). The analysis of elevational limits of tree voles was limited to the Central Cascades Region because tree voles were uncommon or absent in the diet in other regions in the Cascades, regardless of elevation.

Number of Prey Captured Per Year. The estimated mean number of prey captured per year was 271 ± 22 for non-nesting individuals, 543 ± 44 for non-nesting pairs, and 705 ± 57 for nesting pairs with two young (Table 5). Mean estimates for non-nesting individuals ranged from 217–384 prey/yr among regions, or 0.6–1.0 prey items captured/d (Table 5). The only region in which the estimated number of prey captured per year per non-nesting owl was >300, was the Eastern Cascades, which was the only region where the diet included large numbers of insects.

Table 5. Estimated number of prey captured per year by northern Spotted Owls in Oregon, 1970–2003. Numbers under geographic regions indicate the mean number of each prey type captured per individual owl. Numbers in the overall mean columns indicate the mean number of each prey type captured by individuals, non-nesting pairs, and nesting pairs with two young.

PREY ^a	GEOGRAPHIC REGIONS								OVERALL MEAN			
	NORTH		CENTRAL		SOUTH		INTERIOR		CENTRAL		NORTH	
	COAST	COAST	COAST	COAST	COAST	COAST	SOUTHWEST	CASCADES	CASCADES	CASCADES	EAST	CASCADES
Shrews	6.4	2.7	3.2	8.0	6.9	12.8	5.9	6.6	13.1	17.2		
Moles	0.0	0.4	0.1	6.5	2.7	0.0	4.1	2.0	4.0	5.2		
Bats	0.0	0.3	1.1	0.5	1.1	0.0	1.3	0.6	1.2	1.6		
Rabbits/hares	1.8	8.4	9.9	4.9	10.7	0.0	10.8	6.7	13.3	17.4		
American pika	0.0	0.0	0.0	0.2	2.0	0.0	1.1	0.5	0.9	1.3		
Douglas' squirrel	2.2	1.4	0.7	0.4	1.0	0.0	0.4	0.9	1.7	2.3		
Chipmunks	5.4	1.7	1.3	2.6	4.0	4.7	5.2	3.5	7.1	9.1		
N. flying squirrel	107.7	119.8	79.2	61.7	94.0	153.1	113.4	104.1	208.2	270.6		
Gophers	7.1	1.4	0.2	12.0	13.6	0.0	19.9	7.7	15.5	20.0		
Deer mouse	46.8	30.5	14.6	11.9	18.1	0.0	10.8	18.9	37.9	49.1		
Woodrats	24.3	15.1	34.8	46.1	19.4	4.7	11.5	22.3	44.5	58.0		
W. red-backed vole	0.0	5.8	6.6	14.9	31.1	94.8	39.4	27.5	55.0	71.5		
Red tree vole	9.8	38.5	43.1	5.4	23.9	0.0	0.0	17.2	34.5	44.7		
Microtus spp.	0.0	3.2	4.0	6.8	10.9	0.0	5.3	4.3	8.6	11.2		
Other mammals	17.4	9.9	10.1	3.5	7.4	0.0	4.5	7.5	15.1	19.5		
Birds	13.4	12.1	8.6	11.0	8.8	33.3	7.5	13.5	27.0	35.1		
Insects	1.6	8.0	4.8	20.7	12.7	0.0	143.1	27.3	54.5	71.0		
Other	0.9	0.3	0.1	0.1	0.3	0.0	0.2	0.2	0.5	0.5		
Total	244.7	259.4	222.4	217.4	268.6	303.4	384.4	271.4	542.9	705.8		

^a See appendix for complete list of common and scientific names of prey.

DISCUSSION

Composition of the Diet. Our results are similar to previous studies of Spotted Owl diets in Oregon, Washington, and northern California, in that diets were dominated by a few species of mammals, especially flying squirrels, woodrats, tree voles, red-backed voles, and juvenile lagomorphs (e.g., Forsman et al. 1984, 2001, Ward 1990, Cutler and Hays 1991, Hamer et al. 2001). The relative frequency of these mammals in the diet varied among regions, at least partly in response to regional differences in their abundance or distribution (Ward et al. 1998, Carey et al. 1999). Flying squirrels tend to be the most common item in the diet in western Washington and northwestern Oregon, whereas woodrats predominate in diets in southwest Oregon and northern California (Barrows 1980, Ward et al. 1998; Tables 2–3).

In contrast to diets of northern Spotted Owls, diets of Spotted Owls in the southwestern U.S.A. and Mexico tend to include fewer arboreal mammals, and more woodrats, terrestrial small mammals, bats, and insects (e.g., Duncan and Sidner 1990, Ganey 1992, Ward and Block 1995, Smith et al. 1999). These differences are probably due primarily to regional differences in prey availability. For example, flying squirrels are uncommon or absent in the mountains of southern California and the southwestern U.S.A.

As in our study, Smith et al. (1999) found that the majority of insects captured by Spotted Owls were large crickets and beetles. Apparently, these types of insects are easier for Spotted Owls to detect and capture or are taken selectively because of their relatively high biomass per unit effort. However, we also suspect that small, soft bodied insects are generally underestimated in analyses of owl pellets because they are more completely digested. It is possible that the apparent specialization on large insects is at least partially due to this bias.

Mean Prey Size. The mean mass of prey captured in this study and in previous studies of northern Spotted Owls (Ward et al. 1998, Forsman et al. 2001, Hamer et al. 2001) indicated that Spotted Owls feed on larger prey, on average, than most other large owls of the northern hemisphere. For example, the much larger Great Horned Owl (*Bubo virginianus*) and Snowy Owl (*B. scandiaca*), while capable of taking large prey, feed primarily on voles and other small prey in many areas where they occur (Watson 1970, Cromich et al. 2002). In

an area where they were sympatric, Spotted Owls captured larger prey on average than Barred Owls (*Strix varia*; Hamer et al. 2001).

Regional Variation. All studies that have examined variation in diets of Spotted Owls have found differences among regions, territories, years, and seasons (e.g., Forsman et al. 1984, 2001, Laymon 1988, Ward 1990, Ganey 1992, Verner et al. 1992). As discussed by Forsman et al. (1984, 2001), Bull and Henjum (1990), and Ward and Block (1995), there are numerous factors that probably contribute to this variation, including (1) annual, seasonal or local variation in prey abundance, or availability, (2) individual variation in prey selection, (3) small sample size or unequal sampling effort, and (4) biased delivery of large prey to the female and young by nesting males. All of these factors may be important, but there is compelling evidence that spatial and temporal variation in prey populations and selective foraging by the owls are key factors influencing the diet (Forsman et al. 1984, Ward 1990, Carey et al. 1992, Ward and Block 1995, Ward et al. 1998). For example, a number of studies suggest that densities of dusky-footed woodrats and deer mice vary considerably among years (Linsdale and Tevis 1951, Spevak 1983, Ward and Block 1995, Rosenberg et al. 2003), and among and within owl territories (Ward et al. 1998). Carey et al. (1992) found that densities of northern flying squirrels and woodrats were highly variable in sample plots in different Spotted Owl territories in western Oregon.

Some of the regional differences observed in our study suggest interesting hypotheses regarding differences in abundance of small mammals. For example, regional differences in the abundance of red-backed voles in owl diets (Table 2) suggest that red-backed voles are roughly 5–10 times more abundant in the Oregon Cascades than in the central and northern Coast Ranges. However, data from field studies of red-backed voles suggest that they are actually more common in the Coast Ranges than in the Cascades (Aubry et al. 1991). The higher proportions of red-backed voles in owl diets in the Cascades, especially at higher elevations, may be due to prey switching, perhaps in response to lower numbers of alternate prey such as red tree voles at higher elevations (Corn and Bury 1986). It is also possible that terrestrial species like the red-backed vole are more difficult for Spotted Owls to capture in the Coast Ranges than in the Cas-

cares because of the dense brush that covers the ground in many areas in the Coast Ranges.

Timing of Foraging. In our study, and all previous studies of Spotted Owls, the diet was dominated by nocturnal animals, indicating that Spotted Owls forage primarily at night (e.g., Laymon 1988, Cutler and Hays 1991, Ward 1990, Verner et al. 1992, Ward and Block 1995). However, it has been well documented that Spotted Owls do forage during the day, especially if they are feeding fledged young (Miller 1974, Laymon 1988, Sovern et al. 1994). Laymon (1988) even suggested that Spotted Owls with fledged young traveled considerable distances away from their roost areas to forage during the day. However, Forsman et al. (1984), and Sovern et al. (1994) found that Spotted Owls moved very little during the day and that most diurnal foraging involved opportunistic attempts to capture prey near day roosts. Some diurnal prey were probably also captured when they were discovered at night, or when owls were foraging at dawn or dusk.

Seasonal Variation. Predation by Spotted Owls on large mammals and birds was restricted primarily to the spring and summer when large numbers of small, naive juveniles were available (Forsman et al. 1984, 2001, this study). This suggests that adult snowshoe hare, mountain beaver, and grouse are difficult for Spotted Owls to capture. Seasonal predation on juvenile hare and rabbits has been documented in many other owls, including Tawny Owls (*Strix aluco*; Southern 1970), Northern Hawk Owls (*Surnia ulula*; Rohner et al. 1995), Great Gray Owls (*Strix nebulosa*; Mikkola 1983), Barn Owls (*Tyto alba*; Marti 1988), Long-eared Owls (*Asio otus*; Marti 1976), and Snowy Owls (Watson 1970). Forsman et al. (1984) found that diets of northern Spotted Owls during winter became increasingly dominated by arboreal mammals as insects, birds, and juvenile Lagomorphs became less available, and many terrestrial small mammals either became less active above the snow, or went into hibernation.

Numbers of Prey Captured. Based on an analysis of the number of prey in individual pellets, Forsman (1980) estimated that individual Spotted Owls in the central Cascades of Oregon captured 0.7–1.05 prey/d during the fall, winter, and spring (September–April). These estimates, based on a different method than we used in this study, were nearly identical to our present estimate of 0.6–1.0 prey captured/d. Northern Spotted Owls are able

to survive on such a low capture rate because many of the prey they capture are squirrels, woodrats, or lagomorphs that can be stored and eaten in several meals spanning 2 or more d (Forsman et al. 1984).

Prey Selection. Shrews, western red-backed voles, deer mice, and jumping mice are abundant mammals in many forest types in the Pacific Northwest (e.g., Aubry et al. 1991, Corn and Bury 1991, West 1991, Rosenberg et al. 2003, Gomez and Anthony 1998). In most areas they are much more numerous than the flying squirrels, woodrats, lagomorphs, gophers, and tree voles that form the core diet of northern Spotted Owls (Carey et al. 1992, Rosenberg and Anthony 1992, Ward et al. 1998). It is tempting to conclude, therefore, that northern Spotted Owls feed selectively on certain kinds of mammals, especially large mammals that are arboreal or scansorial (Barrows 1980, Forsman et al. 1984, Verner et al. 1992). Ward et al. (1998) presented evidence that Spotted Owls in northern California were preying selectively on large prey, especially woodrats. Ward et al. (1998) further suggested that the energetic reward per unit effort was higher for large prey like woodrats than for smaller prey, and that Spotted Owls were foraging preferentially in areas where woodrats were abundant. However, an alternative hypothesis is that the owls are not selecting for certain kinds of prey, but are simply preying opportunistically on prey that are easiest for them to capture, given the particular morphological attributes of the owl and the structural attributes of the dense forests in which they live. Experimental tests of these hypotheses have not been conducted, but it is obvious that Spotted Owls in the Pacific Northwest rely on a few species of nocturnal mammals for the majority of their food, and that forest management practices that produce healthy populations of these species should benefit Spotted Owls.

ACKNOWLEDGMENTS

This study would not have been possible without the cooperation and assistance of many different biologists and technicians who helped collect, clean, and analyze pellets. In particular, we thank S. Andrews, D. Barrett, M. Broyles, B. Casler, R. Claremont, A. Eldridge, A. Ellingson, R. Forson, L. Gangle, R. Horn, P. Loschl, G. Miller, R. Miller, J. Mires, C. Ogan, F. Oliver, I. Otto, J. Perkins, J. Reid, P. Shacklee, T. Snetsinger, B. Straub, J. Thrailkill, E. Vorisek, and J. Zisa. S.G. Sovern wrote several computer programs that were enormously helpful in analyzing the data. S. Andrews, B. Glenn, P. Loschl, C. Ogan, P. Ward, and an anonymous referee reviewed various drafts of the manuscript. Funding and in-kind support

for this study were provided by the Pacific Northwest and Pacific Southwest Research stations of the U.S. Forest Service, the Oregon State Office of the Bureau of Land Management, the Oregon Department of Forestry, the Oregon Cooperative Fish and Wildlife Research Unit, the Department of Fisheries and Wildlife at Oregon State University, and the Forest and Range Ecosystem Science Center of the U.S. Geological Survey.

LITERATURE CITED

- AUBRY, K.B., M.J. CRITES, AND S.D. WEST. 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. Pages 285–294 in L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff [Eds.], *Wildlife and vegetation of unmanaged Douglas-fir forests*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285, Pacific Northwest Research Station, Portland, OR U.S.A.
- BARROWS, C.W. 1980. Feeding ecology of the Spotted Owl in California. *Raptor Res.* 14:73–77.
- BULL, E.L. AND M.G. HENJUM. 1990. Ecology of the Great Gray Owl. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-265, Pacific Northwest Research Station, Portland, OR U.S.A.
- BURNHAM, K.P., D.R. ANDERSON, AND G.C. WHITE. 1994. Estimation of vital rates of the northern Spotted Owl. Pages 1–44 (Appendix J) in *Final supplemental environmental impact statement on management of habitat for late-successional and old-growth forest related species within the range of the northern Spotted Owl*. Vol. 2. USDA Forest Service, Portland, OR U.S.A.
- CAREY, A.B., S.P. HORTON, AND B.L. BISWELL. 1992. Northern Spotted Owls: influence of prey base and landscape character. *Ecol. Monogr.* 62:223–250.
- , C.C. MAGUIRE, B.L. BISWELL, AND T.M. WILSON. 1999. Distribution and abundance of *Neotoma* in western Oregon and Washington. *Northwest Sci.* 73:65–80.
- CORN, P.S. AND R.B. BURY. 1986. Habitat use and terrestrial activity by red tree voles (*Arborimus longicaudus*) in Oregon. *J. Mammal.* 67:404–406.
- AND ———. 1991. Small mammal communities in the Oregon Coast Range. Pages 241–254 in L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff [Eds.], *Wildlife and vegetation of unmanaged Douglas-fir forests*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285, Pacific Northwest Research Station, Portland, OR U.S.A.
- CROMRICH, L.A., D.W. HOLT, AND S.M. LEASURE. 2002. Trophic niche of North American Great Horned Owls. *J. Raptor Res.* 36:58–65.
- CUTLER, T.L. AND D.W. HAYS. 1991. Food habits of northern Spotted Owls in high elevation forests of Pelican Butte, southwestern Oregon. *Northwest. Nat.* 72:66–69.
- DUNCAN, R.B. AND R. SIDNER. 1990. Bats in Spotted Owl pellets in southern Arizona. *Great Basin Nat.* 50:197–200.
- DUNNING, J.B., JR. (ED.). 1993. *CRC handbook of avian body masses*. CRC Press, Boca Raton, FL U.S.A.
- FORSMAN, E.D. 1980. Habitat utilization by Spotted Owls in the west-central Cascades of Oregon. Ph.D. dissertation, Oregon State Univ., Corvallis, OR U.S.A.
- , E.C. MESLOW, AND H.M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildl. Monogr.* 87.
- , S. DESTEFANO, M.G. RAPHAEL, AND R.J. GUTIÉRREZ (EDS.). 1996. Demography of the northern Spotted Owl. *Stud. Avian Biol.* No. 17.
- , I.A. OTTO, S.G. SOVERN, M. TAYLOR, D.W. HAYS, H. ALLEN, S.L. ROBERTS, AND D.E. SEAMAN. 2001. Spatial and temporal variation in diets of Spotted Owls in Washington. *J. Raptor Res.* 35:141–150.
- FRANKLIN, J.F. AND C.T. DYRNES. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, Pacific Northwest Research Station, Portland, OR U.S.A.
- FRANKLIN, A.B., D.R. ANDERSON, R.J. GUTIÉRREZ, AND K.P. BURNHAM. 2000. Climate, habitat quality, and fitness in northern Spotted Owl populations in northwestern California. *Ecol. Monogr.* 70:539–590.
- GANEY, J.L. 1992. Food habits of Mexican Spotted Owls in Arizona. *Wilson Bull.* 104:321–326.
- GOMEZ, D.M. AND R.G. ANTHONY. 1998. Small mammal abundance in riparian and upland areas of five seral stages in western Oregon. *Northwest Sci.* 72:293–302.
- GOULD, G.I., JR. 1977. Distribution of Spotted Owls in California. *Western Birds* 8:131–146.
- GRABER, R.R. 1962. Food and oxygen consumption in three species of owls (*Strigidae*). *Condor* 64:473–487.
- HAMER, T.E., D.L. HAYS, C.M. SENER, AND E.D. FORSMAN. 2001. Diets of northern Barred Owls and northern Spotted Owls in an area of sympatry. *J. Raptor Res.* 35:221–227.
- HILL, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432.
- LAYMON, S.A. 1988. The ecology of the Spotted Owl in the central Sierra Nevada, California. Ph.D. dissertation, Univ. California, Berkeley, CA U.S.A.
- LINSDALE, J.M. AND L.P. TEVIS, JR. 1951. The dusky-footed woodrat. A record of observations made on the Hastings Natural History Reservation. University California Press, Berkeley, CA U.S.A.
- LOVEJOY, B.P. 1972. The capture-recapture analysis of a mountain beaver population in western Oregon. Ph.D. dissertation, Oregon State Univ., Corvallis, OR U.S.A.
- MARII, C.D. 1976. A review of prey selection by the Long-eared Owl. *Condor* 78:331–336.
- . 1988. A long-term study of food-niche dynamics in the common Barn Owl: comparisons within and between populations. *Can. J. Zool.* 66:1803–1812.
- MASER, C. AND R.M. STORM. 1970. A key to microtinae of the Pacific Northwest. Oregon State Univ. Bookstores, Inc., Corvallis, OR U.S.A.
- MIKKOLA, H. 1983. *Owls of Europe*. Buteo Books, Vermillion, SD U.S.A.

- MILLER, G.M. 1974. Grace M. Miller on Spotted Owls. Pages 130–150 in L.W. Walker [Ed.], *The book of owls*. Alfred A. Knopf, Inc., New York, NY U.S.A.
- MILLER, G.S. 1989. Dispersal of juvenile northern Spotted Owls in western Oregon. M.S. thesis, Oregon State Univ., Corvallis, OR U.S.A.
- , R.J. SMALL, AND E.C. MESLOW. 1997. Habitat selection by Spotted Owls during natal dispersal in western Oregon. *J. Wildl. Manage.* 61:140–150.
- ROHNER, C., J.N.M. SMITH, J. STROMAN, M. JOYCE, F.I. DOYLE, AND R. BOONSTRA. 1995. Northern Hawk-Owls in the nearctic boreal forest; prey selection and population consequences of multiple prey cycles. *Condor* 97:208–220.
- ROSENBERG, D.K. AND R.G. ANTHONY. 1992. Characteristics of northern flying squirrel populations in young, second, and old-growth forests in western Oregon. *Can. J. Zool.* 70:161–166.
- , K.A. SWINDLE, AND R.G. ANTHONY. 2003. Influence of prey abundance on northern Spotted Owl reproductive success in western Oregon. *Can. J. Zool.* 81:1715–1725.
- SMITH, D.G. AND J.R. MURPHY. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. *Brigham Young Univ. Sci. Bull. Biol. Series* 18:69–76.
- SMITH, R.B., M.Z. PEERY, R.T. GUTIÉRREZ, AND W.S. LAHAYE. 1999. The relationship between Spotted Owl diet and reproductive success in the San Bernardino Mountains, California. *Wilson Bull.* 111:22–29.
- SOKAL, R.R. AND F.J. ROHLF. 1969. *Biometry*. W.H. Freeman and Company, San Francisco, CA U.S.A.
- SOUTHERN, H.N. 1970. The natural control of a population of Tawny Owls *Strix aluco*. *J. Zool.* 162:197–285.
- SOVERN, S.G., E.D. FORSMAN, B.L. BISWELL, D.N. ROLPH, AND M. TAYLOR. 1994. Diurnal behavior of the Spotted Owl in Washington. *Condor* 96:200–202.
- SPEVAK, T.A. 1983. Population changes in a Mediterranean scrub rodent assembly during drought. *Southwest. Nat.* 28:47–52.
- THOMAS, J.W., E.D. FORSMAN, J.B. LINT, E.C. MESLOW, B.R. NOON, AND J. VERNER. 1990. A conservation strategy for the northern Spotted Owl: report of the Interagency Scientific Committee to address the conservation of the northern Spotted Owl. USDA Forest Service and USDI Bureau of Land Management, Portland, OR U.S.A.
- THRAILKILL, J.A., R.G. ANTHONY, AND E.C. MESLOW. 1997. An update on demographic estimates for northern Spotted Owls (*Strix occidentalis caurina*) from Oregon's central coast ranges. Pages 432–448 in J.R. Duncan, D.H. Johnson, and T.H. Nicholls [Eds.], *Biology and conservation of owls of the northern hemisphere*. USDA For. Serv. Gen. Tech. Rep. NC-190, North Central Experiment Station, St. Paul, MN U.S.A.
- VERNER, J., R.J. GUTIÉRREZ, AND G.I. GOULD, JR. 1992. The California Spotted Owl: general biology and ecological relations. Pages 55–77 in J. Verner, K.S. McKelvey, B.R. Noon, R.J. Gutiérrez, G.I. Gould, Jr., and T.W. Beck [Eds.], *The California Spotted Owl: a technical assessment of its current status*. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-133, Pacific Southwest Research Station, Berkeley, CA U.S.A.
- VERTS, B.J. AND L.N. CARRAWAY. 1984. Keys to the mammals of Oregon. Oregon State Univ. Bookstores, Inc., Corvallis, OR U.S.A.
- AND ———. 1998. *Land mammals of Oregon*. Univ. California Press, Berkeley, CA U.S.A.
- WARD, J.P., JR. 1990. Spotted Owl reproduction, diet and prey abundance in northwest California. M.S. thesis, Humboldt State Univ., Arcata, CA U.S.A.
- AND W.M. BLOCK. 1995. Mexican Spotted Owl prey ecology. In USDI Fish and Wildl. Serv., *Recovery plan for the Mexican Spotted Owl Vol. 2*. USDI Fish and Wildl. Serv., Albuquerque, NM U.S.A.
- , R.J. GUTIÉRREZ, AND B.R. NOON. 1998. Habitat selection by northern Spotted Owls: the consequences of prey selection and distribution. *Condor* 100:79–92.
- WATSON, A. 1970. The behavior, breeding, and food ecology of the Snowy Owl (*Nyctea scandiaca*). *Ibis* 99:419–462.
- WEATHERS, W.W., P.J. HODUM, AND J.A. BLAKESLEY. 2001. Thermal ecology and ecological energetics of California Spotted Owls. *Condor* 103:678–690.
- WEST, S.D. 1991. Small mammal communities in the southern Washington Cascade Range. Pages 269–283 in L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff [Eds.], *Wildlife and vegetation of unmanaged Douglas-fir forests*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285, Pacific Northwest Research Station, Portland, OR U.S.A.
- ZABEL, C.J., K. MCKELVEY, AND J.P. WARD, JR. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern Spotted Owls (*Strix occidentalis caurina*). *Can. J. Zool.* 73:433–439.

Received 4 April 2003; accepted May 2004

Associate Editor: James R. Belthoff

Appendix. Species, common names, mean mass, activity codes, and total number of prey identified in pellets of northern Spotted Owls in Oregon, 1970–2003.

SPECIES	MEAN MASS (G) ^a	ACTIVITY CODE ^b	N
MAMMALS			22 421
Soricidae			
<i>Sorex bendirii</i> —Pacific water shrew	18 (1)	N, T	7
<i>Sorex monticolus</i> —dusky shrew	6 (1)	N, T	1
<i>Sorex bairdii</i> (<i>obscurus</i>)—Baird’s shrew	9 (1)	N, T	1
<i>Sorex palustris</i> —water shrew	12 (1)	N, T	1
<i>Sorex trowbridgii</i> —Trowbridge’s shrew	5 (1)	N, T	39
<i>Sorex vagrans</i> —vagrant shrew	5 (1)	N, T	8
<i>Sorex pacificus</i> (<i>S. yaquinae</i>)—Pacific shrew	7 (1)	N, T	17
<i>Sorex</i> spp.—unidentified shrew	7 (4)	N, T	243
Talpidae			
<i>Neurotrichus gibbsii</i> —shrew-mole	9 (1)	N, T	68
<i>Scapanus latimanus</i> —broad-footed mole	69 (1)	N, T	7
<i>Scapanus orarius</i> —coast mole	56 (1)	N, T	98
<i>Scapanus</i> spp.—unidentified mole	56 (4)	N, T	66
Chiroptera			
<i>Myotis lucifugus</i> —little brown myotis	6 (1)	N, F	2
<i>Myotis yumanensis</i> —Yuma myotis	6 (1)	N, F	1
<i>Myotis</i> spp.—unidentified myotis	6 (4)	N, F	3
<i>Lasionycteris noctivagans</i> —silver-haired bat	11 (1)	N, F	5
<i>Eptesicus fuscus</i> —big brown bat	15 (1)	N, F	7
Unidentified bat	10 (4)	N, F	49
Ochotonidae			
<i>Ochotona princeps</i> —American pika	171 (1)	B, T	85
Leporidae			
<i>Sylvilagus bachmani</i> —brush rabbit	50–750 (3)	B, T	224
<i>Lepus americanus</i> —snowshoe hare	50–1400 (3)	B, T	528
Unidentified rabbit/hare	50–900 (3)	B, T	258
Aplodontidae			
<i>Aplodontia rufa</i> —mountain beaver	100–550 (3)	N, T	56
Sciuridae			
<i>Tamias amoenus</i> —yellow-pine chipmunk	48 (1)	D, S	2
<i>Tamias townsendii</i> —Townsend’s chipmunk	83 (1)	D, S	203
<i>Tamias senex</i> —Allen’s chipmunk	85 (1)	D, S	21
<i>Tamias</i> spp.—unidentified chipmunk	83 (4)	D, S	26
<i>Spermophilus beecheyi</i> —California ground squirrel	626 (1)	D, T	2
<i>S. lateralis</i> —golden-mantled ground squirrel	169 (1)	D, T	1
<i>Sciurus griseus</i> —western gray squirrel	60–795 (3)	D, A	15
<i>Tamiasciurus douglasii</i> —Douglas’ squirrel	221 (1)	D, A	103
<i>Glaucomys sabrinus</i> —northern flying squirrel	130 (1)	N, A	8826
Unidentified Sciurid spp.	130 (4)	U, S	17
Geomyidae			
<i>Thomomys bottae</i> —Botta’s pocket gopher	142 (1)	N, T	2
<i>Thomomys mazama</i> —western pocket gopher	95 (1)	N, T	435
<i>Thomomys talpoides</i> —northern pocket gopher	102 (1)	N, T	7
<i>Thomomys</i> spp.—unidentified gopher	95 (4)	N, T	145
Muridae—Sigmodontinae			
<i>Peromyscus maniculatus</i> —deer mouse	22 (1)	N, T	1830
<i>Neotoma cinerea</i> —bushy-tailed woodrat	284 (1)	N, S	512

Appendix. Continued.

SPECIES	MEAN MASS (G) ^a	ACTIVITY CODE ^b	N
<i>Neotoma fuscipes</i> —dusky-footed woodrat	286 (1)	N, S	529
<i>Neotoma</i> spp.—unidentified woodrat	285 (4)	N, S	2258
Muridae—Murinae			
<i>Rattus rattus</i> —black rat	250 (3)	N, T	5
Muridae—Arvicolinae			
<i>Clethrionomys californicus</i> —western red-backed vole	23 (1)	N, T	1491
<i>Phenacomys intermedius</i> —heather vole	28 (1)	N, T	10
<i>Arborimus albipes</i> —white-footed vole	23 (1)	N, T	5
<i>Arborimus longicaudus</i> —red tree vole	26 (1)	N, A	2954
<i>Microtus californicus</i> —California vole	43 (1)	N, T	19
<i>Microtus canicaudus</i> —gray-tailed vole	36 (1)	N, T	6
<i>Microtus longicaudus</i> —long-tailed vole	56 (1)	N, T	28
<i>Microtus oregoni</i> —creeping vole	20 (1)	N, T	187
<i>Microtus richardsoni</i> —Richardson’s vole	70 (1)	N, T	45
<i>Microtus townsendii</i> —Townsend’s vole	54 (1)	N, T	25
<i>Microtus</i> spp.—unidentified vole	30 (4)	N, T	143
Muridae spp.—unidentified vole/mouse	25 (4)	U, U	616
Dipodidae			
<i>Zapus trinotatus</i> —Pacific jumping mouse	24 (1)	N, T	54
<i>Zapus princeps</i> —western jumping mouse	30 (1)	N, T	2
Procyonidae			
<i>Bassariscus astutus</i> —ringtail	200–400 (3)	N, S	5
Mustelidae			
<i>Mustela erminea</i> —ermine	55 (1)	N, T	43
<i>Mustela frenata</i> —long-tailed weasel	110 (3)	N, T	2
Mephitidae			
<i>Spilogale gracilis</i> —spotted skunk	500 (3)	N, T	1
Unidentified mammals	30–400 (3)	U, U	67
BIRDS			1042
Anatidae			
<i>Aix sponsa</i> —Wood Duck	658 (2)	D, F	1
Anatidae spp.—unidentified duck	658 (4)	D, F	3
Phasianidae			
<i>Bonasa umbellus</i> —Ruffed Grouse	100–576 (3)	D, F	11
<i>Dendragapus obscurus</i> —Blue Grouse	500–890 (3)	D, F	2
Grouse spp.	100–600 (3)	D, F	7
Odontophoridae			
<i>Oreortyx pictus</i> —Mountain Quail	224 (2)	D, F	10
Columbidae			
<i>Patagioenas fasciata</i> —Band-tailed Pigeon	392 (2)	D, F	1
Strigidae			
<i>Asio otus</i> —Long-eared Owl	262 (2)	N, F	1
<i>Strix occidentalis</i> —Spotted Owl	610 (2)	N, F	3
<i>Megascops kennicottii</i> —Western Screech Owl	169 (2)	N, F	59
<i>Glaucidium gnoma</i> —Northern Pygmy Owl	68 (2)	N, F	21
<i>Aegolius acadicus</i> —Northern Saw-whet Owl	83 (2)	N, F	44
Strigidae spp.—unidentified small owl	124 (4)	N, F	4

Appendix. Continued.

SPECIES	MEAN MASS (G) ^a	ACTIVITY CODE ^b	N
Picidae			
<i>Colaptes auratus</i> —Northern Flicker	142 (2)	D, F	30
<i>Sphyrapicus ruber</i> —Red-breasted Sapsucker	49 (2)	D, F	22
<i>Picoides albolarvatus</i> —White-headed Woodpecker	61 (2)	D, F	1
<i>Picoides arcticus</i> —Black-backed Woodpecker	69 (2)	D, F	1
<i>Picoides pubescens</i> —Downy Woodpecker	50 (2)	D, F	1
<i>Picoides villosus</i> —Hairy Woodpecker	66 (2)	D, F	9
<i>Dryocopus pileatus</i> —Pileated Woodpecker	287 (2)	D, F	6
Picidae spp.—unidentified Woodpecker	106 (4)	D, F	2
Tyrannidae			
<i>Contopus cooperi</i> —Olive-sided Flycatcher	32 (2)	D, F	2
Corvidae			
<i>Cyanocitta stelleri</i> —Steller’s Jay	128 (2)	D, F	83
<i>Perisoreus canadensis</i> —Gray Jay	73 (2)	D, F	12
Paridae			
<i>Poecile rufescens</i> —Chestnut-backed Chickadee	10 (2)	D, F	4
Certhiidae			
<i>Certhia americana</i> —Brown Creeper	8 (2)	D, F	4
Sittidae			
<i>Sitta canadensis</i> —Red-breasted Nuthatch	10 (2)	D, F	8
Troglodytidae			
<i>Troglodytes troglodytes</i> —Winter Wren	9 (2)	D, F	5
Regulidae			
<i>Regulus calendula</i> —Ruby-crowned Kinglet	7 (2)	D, F	2
<i>Regulus satrapa</i> —Golden-crowned Kinglet	6 (2)	D, F	3
Turdidae			
<i>Catharus ustulatus</i> Swainson’s Thrush	31 (2)	D, F	2
<i>Catharus guttatus</i> —Hermit Thrush	31 (2)	D, F	5
<i>Ixoreus naevius</i> —Varied Thrush	78 (2)	D, F	19
<i>Turdus migratorius</i> —American Robin	77 (2)	D, F	12
<i>Turdus/Ixoreus</i> spp.—thrush/robin spp.	78 (4)	D, F	101
Bombycillidae			
<i>Bombycilla cedrorum</i> —Cedar Waxwing	32 (2)	D, F	1
Parulidae			
<i>Dendroica occidentalis</i> —Hermit Warbler	9 (2)	D, F	4
<i>Dendroica</i> spp.—unidentified warbler	10 (4)	D, F	1
Thraupidae			
<i>Piranga ludoviciana</i> —Western Tanager	28 (2)	D, F	4
Emberizidae			
<i>Pipilo maculatus</i> —Spotted Towhee	40 (2)	D, F	6
<i>Passerella iliaca</i> —Fox Sparrow	32 (2)	D, F	1
<i>Junco hyemalis</i> —Dark-eyed Junco	18 (2)	D, F	8
Cardinalidae			
<i>Pheucticus melanocephalus</i> —Black-headed Grosbeak	42 (2)	D, F	1

Appendix. Continued.

SPECIES	MEAN MASS (G) ^a	ACTIVITY CODE ^b	N
Fringillidae			
<i>Carpodacus purpureus</i> —Purple Finch	25 (2)	D, F	1
<i>Carpodacus</i> spp.—unidentified finch	30 (4)	D, F	1
<i>Loxia curvirostra</i> —Red Crossbill	36 (2)	D, F	4
<i>Carduelis tristis</i> —American Goldfinch	13 (2)	D, F	1
<i>Coccothraustes vespertinus</i> —Evening Grosbeak	64 (2)	D, F	13
Unidentified birds			
Large bird	300–1000 (3)	U, F	6
Medium-size bird	60–299 (3)	U, F	185
Small bird	5–59 (3)	D, F	304
AMPHIBIANS			7
<i>Rana</i> spp.—frog spp.	30 (6)	B, T	7
REPTILES			12
<i>Elgaria coerulea</i> —northern alligator lizard	35 (6)	D, T	1
<i>Sceloporus occidentalis</i> —western fence lizard	10 (6)	D, T	2
<i>Thamnophis ordinoides</i> —northwestern garter snake	100 (6)	D, T	1
<i>Thamnophis</i> spp.—garter snake spp.	100 (6)	D, T	2
Unidentified snake	100 (4)	D, T	6
MOLLUSCS—GASTROPODA (Terrestrial snails)			7
<i>Haplotrema vancouverense</i>	7 (6)	B, T	2
<i>Monedenia fidelis</i>	5 (6)	B, T	2
Unidentified snail	5 (4)	B, T	3
INSECTS			1005
Orthoptera—Tettigoniidae (Camel crickets)			
<i>Cyphoderris monstrosa</i> —great grig	2.0 (5)	N, S	412
Orthoptera—Blattidae			
<i>Cryptocercus punctulatus</i> —wood-feeding cockroach	1.0 (5)	U, T	5
<i>Parcoblatta</i> spp. wood roach	1.0 (5)	N, T	1
Orthoptera spp.	1.0 (5)	U, U	2
Hemiptera—Pentatomidae (stink bugs)			
<i>Chlorochroa</i> spp.	0.3 (5)	U, U	1
Homoptera—Cicadidae (cicadas)			
<i>Okanagana</i> spp.	0.4 (5)	U, U	5
Neuroptera—Corydalidae (nerve-winged insects)			
<i>Dysmichohermes disjunctus</i>	2.0 (5)	N, U	4
Neuroptera—Raphidiidae (snakeflies)			
Raphidiidae spp.	0.2 (5)	U, U	3
Coleoptera—Cicindelidae (tiger beetles)			
<i>Omus californicus</i>	0.5 (5)	U, U	1
<i>Omus dejeani</i>	0.5 (5)	U, U	1
Coleoptera—Carabidae (ground beetles)			
<i>Pterostichus amethystinus</i>	0.3 (5)	U, U	1
<i>Pterostichus lama</i>	0.3 (5)	U, U	7
<i>Pterostichus neobrunneus</i>	0.3 (5)	U, U	1
<i>Pterostichus</i> spp.	0.3 (5)	U, U	1
<i>Scaphinotus</i> spp.	0.3 (5)	U, U	1

Appendix. Continued.

SPECIES	MEAN MASS (G) ^a	ACTIVITY CODE ^b	N
Coleoptera—Scarabaeidae (dung beetles)			
<i>Bolboceras obesus</i>	0.3 (5)	U, U	1
<i>Pleocomma dubitalis</i>	0.3 (5)	U, U	10
Coleoptera—Lucanidae (stag beetles)			
<i>Ceruchus striatus</i>	0.5 (5)	U, U	1
<i>Sinodendron rugosum</i>	0.5 (5)	U, U	4
Coleoptera—Buprestidae (metallic woodborers)			
<i>Buprestis aurulenta</i>	0.3 (5)	U, U	1
Coleoptera—Elateridae (click beetles)			
<i>Ctenicera</i> spp.	0.3 (5)	U, U	1
Coleoptera—Tenebrionidae (darkling beetles)			
<i>Iphthimus serratus</i>	0.5 (5)	U, U	1
<i>Helops</i> spp.	0.5 (5)	U, U	1
Coleoptera—Cerambycidae (long-horned woodborers)			
<i>Ergates spiculatus</i> —ponderous borer	3.0 (5)	N, U	249
<i>Prionus californicus</i> —giant root borer	2.0 (5)	U, U	5
<i>Acmaeops proteus</i>	0.5 (5)	U, U	1
<i>Centrodera spurca</i>	0.5 (5)	U, U	2
<i>Plectrura spinicauda</i>	0.5 (5)	U, U	1
Coleoptera—Curculionidae (weevils)			
<i>Dyslobus lecontei</i>	0.3 (5)	U, U	3
<i>Dyslobus</i> spp.	0.3 (5)	U, U	10
<i>Panscopus</i> spp.	0.3 (5)	U, U	1
Coleoptera spp.—unidentified beetles	0.3 (5)	U, U	11
Lepidoptera—unidentified moths	0.5 (5)	U, U	2
Hymenoptera—Formicidae (ants)			
<i>Camponotus</i> spp.	0.1 (5)	U, U	12
<i>Formica fusca</i>	0.1 (5)	U, U	1
Formicidae spp.	0.1 (5)	U, U	1
Hymenoptera—Vespidae (hornets and yellowjackets)			
<i>Dolichorespula maculata</i>	0.1 (5)	U, U	1
Unidentified large insect	2.0 (5)	U, U	21
Unidentified small insect	0.3 (5)	U, U	218
CRUSTACEANS			
<i>Pacifastacus leniusculus</i> —crayfish	20 (6)	B, T	2
ARACHNIDA			
<i>Uroctonus mordax</i> —scorpion	3 (5)	N, T	1

^a Source of mass estimate is in parentheses: 1 = Verts and Carraway 1998; 2 = Dunning 1993; 3 = mass of each individual estimated based on comparison with reference specimens of known mass; 4 = mean of all species in group, 5 = means based on estimates from similar species in this genus or group; 6 = estimates from local specimens.

^b First letter indicates primary period of activity (D = diurnal, N = nocturnal, B = active both day and night, U = unknown). Second letter indicates primary area of activity (T = terrestrial, A = arboreal, S = scansorial, F = flying or aerial animal, U = unknown).

^c Verts and Carraway (1998) split the “*Tamias townsendii* Complex” into three species, but we treated all *Tamias* species west of the crest of the Cascades as one species, because we could not tell them apart based on bone fragments in pellets.

A COMPARISON OF BARRED AND SPOTTED OWL NEST-SITE CHARACTERISTICS IN THE EASTERN CASCADE MOUNTAINS, WASHINGTON

JOSEPH B. BUCHANAN¹

Washington Department of Fish and Wildlife, 600 Capitol Way North, Olympia, WA 98501 U.S.A.

TRACY L. FLEMING

National Council for Air and Stream Improvement, 23308 N.E. 148th, Brush Prairie, WA 98606 U.S.A.

LARRY L. IRWIN

National Council for Air and Stream Improvement, P.O. Box 68, Stevensville, MT 59870 U.S.A.

ABSTRACT.—We describe 10 nest sites of the northern Barred Owl (*Strix varia varia*) in mixed-coniferous forests of the eastern Cascades in Washington, a region where the species is sympatric with the northern Spotted Owl (*S. occidentalis caurina*). Our goal was to determine whether Barred and Spotted owls used similar habitats for nesting. In contrast to Spotted Owls, Barred Owl nest sites were situated on gentle slopes or flat ground, closer to water, and included more hardwoods and a greater richness of tree species. Barred Owl nests were usually in cavities or platforms created at the broken top of the tree bole. Only two Barred Owl nests were in abandoned hawk nests or clumps of branches infected by dwarfmistletoe (*Arceuthobium douglasii*), which were the two most common nest structures used by Spotted Owls in our study area. Barred Owls used a greater range of tree species for nesting, including three nests in black cottonwoods (*Populus trichocarpa*), a species rarely used for nesting by Spotted Owls in the Pacific Northwest. Although differences in these attributes suggest that the two species used somewhat different habitats, Barred Owls have become more abundant in our study area and the region, and further assessments of habitat use may indicate greater niche overlap.

KEY WORDS: *northern Barred Owl*; *Strix varia*; *northern Spotted Owl*; *Strix occidentalis*; *habitat*; *nest sites*; *Washington*.

UNA COMPARACIÓN LAS CARACTERÍSTICAS DEL NIDO *STRIX VARIA VARIA* Y *STRIX OCCIDENTALIS CAURINA* EN LAS MONTAÑAS DE EASTERN CASCADE, WASHINGTON

RESUMEN.—Describimos diez sitios de nido de *Strix varia* en bosques mixtos de coníferas de las montañas Eastern Cascade en Washington, una región donde la especie es simpátrica con *S. occidentalis caurina*. Nuestro objetivo era el de determinar si *Strix varia varia* y *Strix occidentalis caurina*, utilizan habitats similares para anidar. En contraste a *S. occidentalis caurina* los sitios de los nidos de *S. varia varia* estaban ubicados en pendientes suaves o en pastizales planos, cerca del agua e incluían mas maderas duras y una mayor riqueza de especies de árboles. Los nidos de *S. varia varia* estaban ubicados en cavidades o en plataformas creadas por árboles quebrados en su parte superior del tronco. Tan solo dos nidos de *S. varia varia* se encontraban en nidos abandonados de gavilanes o en el follaje de ramas infectadas por *Arceuthobium douglasii*, las cuales fueron las estructuras mas comunes utilizadas por *S. occidentalis caurina* en nuestra area de estudio. *S. varia varia* utilizo un mayor rango de especies de árboles para anidar, incluyendo a *Populus trichocarpa* una especie raramente utilizada para anidar por *S. occidentalis caurina* en el Noreste Pacifico. Aunque las diferencias en estos atributos sugieren que de algún modo las dos especies utilizan diferentes habitats, *S. varia varia* se ha vuelto mas abundante en nuestra área de estudio y en la región. Una evaluación posterior del uso de hábitat puede indicarnos un mayor traslape de nicho.

[Traducción de César Márquez]

¹ E-mail address: buchajbb@dfw.wa.gov

Until recently, the range of the northern Barred Owl (*Strix varia varia*) was limited to the hardwood and mixed conifer/hardwood forests of eastern North America (Mazur and James 2000). In the last century, Barred Owls expanded their range westward across the continent to British Columbia (Grant 1966) and then south to central California (e.g., Taylor and Forsman 1976, Leder and Walters 1980, Dark et al. 1998). Barred Owls are now sympatric with northern Spotted Owls (*S. occidentalis caurina*) over nearly the entire range of the latter species (Dark et al. 1998). The continuing range expansion and increase in population density of Barred Owls in the Pacific Northwest has raised concerns because they may compete with Spotted Owls (USDI 1992, Kelly et al. 2003), and the two species hybridize (Hamer et al. 1994, Kelly 2001). The effects of competition and hybridization on the Spotted Owl, a threatened species (USDI 1990), are unknown but potentially deleterious (see Pearson and Livezey 2003).

Stand- and landscape-level habitat relationships of Barred Owls have been documented in other parts of their range (e.g., Nicholls and Warner 1972, Apfelbaum and Seelbach 1983, McGarigal and Fraser 1984, Bosakowski et al. 1987). In Washington, landscape composition of stand types or forest age classes associated with nesting Barred Owls have been described in the northwestern and southwestern Cascades (Hamer 1988, Pearson and Livezey 2003) and the central eastern Cascades (Herter and Hicks 2000), areas where both Barred Owls and Spotted Owls occur. In this paper, we describe attributes of sites used for nesting by sympatric Barred and Spotted owls in the eastern Cascade Mountains.

STUDY AREA

Our study area was the east slope of the Cascade Mountains in Washington. The 875 000-ha area extends ca. 225 km in a north-south direction, from Canada to the Oregon border, up to 45 km eastward from the Cascade crest, and includes the Wenatchee and Okanogan National Forests, portions of the Gifford Pinchot National Forest, tribal lands of the Yakama Nation, and adjacent state and private lands. The study area contains forest associations ranging from the moist Douglas-fir (*Pseudotsuga menziesii*)/western hemlock (*Tsuga heterophylla*) zone in the west to the xeric ponderosa pine (*Pinus ponderosa*)/artemesia zone in the east (Franklin and Dyrness 1973), and contains coniferous and mixed-coniferous forests (Cobb 1988). Fire suppression in the last century has changed the structure and composition of forests in parts of the region (Agee 1993).

METHODS

Between 1988 and 1994, we visited all known Barred Owl nests in our study area, except for one nest that was reported to us but located in an extremely remote area. Biologists found nests of both species during timber-sale evaluations, Spotted Owl surveys, or in the case of some Barred Owl sites, during specific searches for their nests.

At each nest, we described the nest and nest tree. This information included the species, age (based on an increment core extracted at breast height), diameter at breast height (DBH), height, canopy position, condition of the nest tree (i.e., alive or dead; top intact or broken), and the nest type (i.e., cavity, broken-top platform, abandoned hawk nest, cluster of mistletoe-infected branches), height, and orientation relative to the tree trunk.

Vegetation structure at nest sites was quantified in a single 0.10-ha circular plot (18.0-m radius) centered on the nest tree and five 0.04-ha plots (11.4-m radius). The middle 0.04-ha plot was centered on the nest tree and the others were immediately adjacent in the cardinal directions (Buchanan et al. 1995). Characteristics of snags and three dominant or codominant and three intermediate trees (tree height, canopy height, age) were assessed in the 0.10-ha plot. Snags were measured (DBH, height) and identified to species and decay class (Cline et al. 1980). In the 0.04-ha plots we identified and measured all trees ≥ 10 cm DBH, estimated the volume of coarse woody debris according to four decay classes (Solins 1982), and counted the number of saplings < 10 cm DBH. We measured canopy closure at Barred Owl nests using a spherical densiometer (Lemmon 1956). We were unable to make comparisons of canopy closure to the paired sample of Spotted Owl sites; instead, we compared our sample to a previously-documented sample of owl nests that characterized the region (Buchanan et al. 1993, 1995).

At each nest site, we described site disturbance and topographic features such as elevation, slope, topographic position, and aspect. Site disturbance was indicated by the presence of fire scars on logs or trees, or by evidence of timber harvest. Because Barred Owls often use lowland forests near water in other parts of their range (Mazur and James 2000), we estimated the distance to nearest water channels ≥ 5 -m wide or ponds ≥ 2 ha and evaluated whether Barred Owl nest sites had different geophysical attributes than sites in which Spotted Owls nested. A complete description of data collection procedures is found in Buchanan et al. (1993, 1995).

We compared site and vegetation attributes at Barred Owl nests with a sample of Spotted Owl nests from a previous investigation (Buchanan et al. 1993, 1995). The forest-stand characteristics of Spotted Owl nest sites in the Eastern Cascades province vary intra-regionally (Buchanan and Irwin 1998). Much of this variation is related to the moisture gradient and concomitant changes in forest association across the region, and has been described in the context of Fire Management Analysis Zones (FMAZ), a geographic analysis and management system the U.S. Forest Service uses for fire management on the Wenatchee National Forest (Buchanan and Irwin 1998). Consequently, each Barred Owl nest was paired with a randomly-selected Spotted Owl nest from the same FMAZ, except for a nest in Klickitat County that was

paired with a Spotted Owl nest from that region. The pool of available Spotted Owl nests included 80 sites well distributed throughout the Wenatchee National Forest and vicinity (FMAZ 1 = 14 sites, FMAZ 2 = 31 sites, FMAZ 3 = 19 sites, FMAZ 4 = 13 sites, FMAZ 5 = 3 sites; Buchanan and Irwin 1998) and 31 sites in Klickitat County and vicinity (J. Buchanan unpubl. data).

We used a two-step approach to analyze our data. First, we used paired *t*-tests (Zar 1984) to determine if habitat features at Barred Owl nest sites differed from those at Spotted Owl sites. Percent-slope values were arc-sine transformed prior to analysis. The Wilcoxon test was used to compare the number of tree species present at nests of the two species. Means \pm SE are presented unless otherwise indicated; *df* = 9 in all comparisons. We considered statistical tests significant when $\alpha \leq 0.1$.

Second, because of the possibility that some of our significant findings were the product of chance because of the large number of paired comparisons, we used logistic regression (Hosmer and Lemeshow 1989) to determine whether our significant variables would be included in multivariate models. For this analysis we included all variables with *P*-values ≤ 0.25 in the univariate analyses (see Mickey and Greenland 1989) and produced a set of all possible models using those variables. We evaluated the resulting models to identify variables that contributed to high rates of correct sample classification. We did not intend the models to be used as predictive tools because of our concern that habitat use by Barred Owls has likely changed, thus necessitating the development of new models (see below).

RESULTS

General Site Characteristics. We quantified habitat at 10 Barred Owl nest sites in the eastern Cascades province. These sites were 0.4–12.5 km (\bar{x} = 4.8 \pm 1.4 km) from known Spotted Owl nest locations. Nine sites occurred in four of the five fire management analysis zones (zone 1 = three sites, zone 2 = two sites, zone 3 = three sites, zone 5 = one site) and one site was in Klickitat County.

Barred Owl nests were generally in areas with low relief (\bar{x} slope = 10.6 \pm 4.1%) in bottomlands (7), on a mid-slope bench (1), a ridge-top (1), or at the base of a gradual slope (1). Spotted Owls nested on significantly steeper terrain (\bar{x} slope = 41.9 \pm 4.5%; *t* = 5.19, *P* < 0.0001). Because the terrain at several Barred Owl nests was level, we did not calculate site aspect. Elevation of Barred Owl sites ranged from 320–1180 m (\bar{x} = 781 \pm 84.6 m) and did not differ from Spotted Owl nest sites (\bar{x} = 913 \pm 54.8 m; *t* = 1.31, *P* = 0.21). Barred Owl nests were closer to water (\bar{x} = 448 \pm 183.2 m) than those of Spotted Owls (\bar{x} = 1993 \pm 534.1 m; *t* = 2.74, *P* = 0.01).

There was little evidence of recent fire or logging activity at Barred Owl nests, but most sites had

Table 1. Mean age and size attributes of Barred Owl (*N* = 10) and Spotted Owl (*N* = 10) nest trees in the eastern Cascade Mountains, WA. Analysis results based on paired *t*-tests with *df* = 9.

ATTRIBUTE	BARRED OWL NESTS		SPOTTED OWL NESTS		<i>t</i>	<i>P</i>
	\bar{x}	SE	\bar{x}	SE		
DBH (cm)	106.0	15.4	64.9	8.1	2.36	0.03
Age (yr)	216.8	58.0	181.9	60.6	0.42	0.68
Tree height (m)	25.1	2.6	30.5	3.3	1.30	0.21
Nest height (m)	16.4	1.2	16.6	1.9	0.12	0.91

been disturbed by these activities decades prior to known owl use. Evidence of fire (in the form of fire scars on trunks) was present at nine of 10 Barred Owl sites and six of 10 Spotted Owl sites. A slash fire burned at one Barred Owl site the year prior to nest use. Five of 10 Barred Owl sites had been lightly harvested; one site was logged several years prior to use and the others apparently several decades earlier. Four of 10 Spotted Owl sites exhibited evidence of selective timber harvest several decades prior to use.

Nests and Nest Trees. There were a number of differences between the two owl species in nest tree attributes. Barred Owl nests were located in five tree species, including three in black cottonwoods (*Populus trichocarpa*), three in Douglas-firs, two in grand firs (*Abies grandis*), one in a western hemlock, and one in a western larch (*Larix occidentalis*). In contrast, nine of 10 Spotted Owl nests were in Douglas-firs. Of the 10 Barred Owl nests, two were in living and intact trees, and eight were in trees that had broken boles (six alive, two dead). In comparison, seven Spotted Owl nest trees were alive and intact, and three were either dead or had broken tops. Barred Owl nest trees were significantly larger in diameter (at breast height) than Spotted Owl nest trees, but there were no differences in tree age, tree height, or height of nest above the ground (Table 1).

The two owl species exhibited differences in the types of nests used. Eight Barred Owl nests were in cavities or on chimney-like platforms created at the point where the tree bole had broken; one was in a clump of branches infected by dwarfmistletoe (*Arceuthobium douglasii*), and one was an abandoned Northern Goshawk (*Accipiter gentilis*) nest. Only two Spotted Owl nests were in cavities or on

Table 2. Mean structural and age attributes of vegetation at Barred Owl ($N = 10$) and Spotted Owl ($N = 10$) nest sites in the Eastern Cascade Mountains, WA. Analysis results based on paired t -tests with $df = 9$.

ATTRIBUTE	BARRED OWL NESTS		SPOTTED OWL NESTS		t	P
	\bar{x}	SE	\bar{x}	SE		
Age of dominant/codominant trees (yr)	164.4	41.0	191.9	62.1	0.37	0.71
Age of intermediate trees (yr)	88.7	18.2	108.0	17.4	0.77	0.45
Basal area of conifers (m ² /ha)	44.2	9.0	42.5	6.2	0.16	0.87
Basal area of Douglas-firs (m ² /ha)	15.1	4.1	22.8	3.5	1.43	0.17
Basal area of hardwoods (m ² /ha)	7.8	4.0	0.21	0.1	1.9	0.07
Basal area of all trees (m ² /ha)	52.1	8.1	42.7	6.1	0.93	0.37
Basal area of snags (m ² /ha)	6.3	1.8	14.6	4.1	1.84	0.08
Height (m) to base of canopy (dominants/codominants)	12.8	1.8	16.6	1.0	1.84	0.08
Height (m) to base of canopy (intermediate trees)	8.5	1.3	8.7	1.3	0.09	0.93
Height (m) of dominant/codominant trees	31.2	1.6	33.8	0.9	1.42	0.17
Height (m) of intermediate trees	20.3	1.5	21.1	1.2	0.40	0.69
Sapling abundance (0.04 ha)	20.7	3.6	13.3	2.9	1.63	0.12

broken tops. The others were in clumps of branches infected by dwarfmistletoe or abandoned goshawk nests.

Vegetation Structure. With few exceptions, there were no differences between species in the vegetation structure we measured at owl nests. Barred Owl sites had a lower height to the base of the canopy of dominant/codominant trees, a greater basal area of hardwood trees, and a lower basal area of snags (Table 2). Other measures of tree height, canopy height, basal area, or sapling abundance did not differ between the two owl species (Table 2). Canopy closure at five Barred Owl sites averaged 70.6%, which is within the range reported from the eastern Cascade Mountains (Buchanan and Irwin 1998).

We recorded 16 tree species at the Barred Owl nest sites, although seven of these were present at two sites only. At the Spotted Owl nest sites, we observed 8 tree species including three species present at ≤ 2 sites. Four species were present at ≥ 5 Barred Owl sites: Douglas-fir, grand fir, western redcedar (*Thuja plicata*), and red alder (*Alnus rubra*); and Douglas-fir and grand fir were present at ≥ 8 sites. The latter two species were equally prevalent at Spotted Owl sites ($N = 10$ and $N = 7$, respectively); ponderosa pine was the only other species present at ≥ 5 Spotted Owl sites ($N = 6$). Hardwoods were present at seven Barred Owl sites and three Spotted Owl sites. The median number

of tree species present at Barred Owl nest sites ($N = 5$) was greater than at Spotted Owl nests ($N = 3$; Wilcoxon $Z = 3.53$, $P = 0.0004$).

Logistic-regression analyses identified a number of models that classified nest sites with a high degree of accuracy. Fourteen models correctly classified ≥ 18 of 20 nest sites, including six models that correctly classified ≥ 19 sites. Five of the six parameters that were significant in our paired analyses were identified in the latter six models: *percent slope* and *number of tree species* (included in four models); *distance to water* (three models), *basal area of hardwoods*, and *basal area of snags* (two models); and *height of dominant/co-dominant trees* (one model).

DISCUSSION

Many studies have documented that Barred Owls inhabit or associate with forests containing standing water or wetlands (e.g., Nicholls and Warner 1972, Devereaux and Mosher 1984, Bosakowski et al. 1987). Falk (1990) reported no association of Barred Owl nest sites in Connecticut with water, although there was significantly more water in the vicinity of nests compared to two diurnal raptors included in that study.

In the eastern Cascade Mountains of Washington, Barred Owl nests were much closer to water and were in valleys or other areas with less relief than were nests of Spotted Owls. An apparent preference for areas near water by Barred Owls may be

related to the greater diversity of small mammal (Peffer 2001) and aquatic prey species associated with riparian zones within the eastern Cascades. In addition, the prevalence of Barred Owl sites in bottomlands likely influenced the greater richness of tree species and the greater abundance of hardwoods that we observed compared to Spotted Owl nests.

We found two substantial differences between these owl species in the type of nest structures and the size of nest trees used. First, Barred Owls most often used cavities or platforms atop broken tree boles and infrequently used old goshawk nests or clusters of branches infected by mistletoe. In contrast, most Spotted Owl nests were associated with mistletoe or old goshawk nests (Buchanan et al. 1993), a use pattern that appears to be unique to the eastern Cascades and the Klamath Mountains in Oregon (Forsman et al. 1984). Barred Owls may use nest structures opportunistically; however, all six nests Yannielli (1991) found in Connecticut were in cavities. On the other hand, 18 of 38 (47%) nests reported by Bent (1938) were abandoned hawk nests. This pattern of nest use is consistent with the generalist nature of this species in western North America (Mazur and James 2000).

Second, Barred Owl nest trees were larger than those Spotted Owls used in our study area. This difference can be explained by: (1) Barred Owl use of cottonwoods, which rapidly attain large size, (2) the generally larger size of trees on gentle terrain and in bottomlands, where growing conditions are better than on the sloping terrain where Spotted Owls nested (Buchanan et al. 1995), and (3) the comparatively greater Barred Owl use of cavity and broken-top platform structures, which occur in larger trees than the goshawk or mistletoe nests that Spotted Owls used (Buchanan et al. 1993). Although Barred Owls are larger than Spotted Owls (Snyder and Wiley 1976), it is unknown if the former requires a larger cavity for nesting. The comparatively lower basal area of snags at Barred Owl nests might be explained by this species' use of varied habitats and prey.

The availability of nest sites and prey are thought to be primary factors that limit raptor populations (Newton 1979, Nelson 1983). Therefore, competition between raptor species likely involves significant mutual reliance on one or both of these resources. Hamer et al. (2001) suggested that competition between Barred and Spotted owls for

prey may occur in the northern Cascades Region in western Washington.

Despite the differences we found in habitat use, a number of habitat attributes were common to the two species and suggest a certain amount of niche overlap. All Barred Owl nests were within the geographic range of the Spotted Owl and occurred within the elevation range and forest associations Spotted Owls use on the east slope of the Cascade Mountains in Washington. There were no interspecific differences in total heights of dominant or intermediate trees, or in the basal area of trees; also, there did not appear to be differences in canopy closure. In short, both species primarily nested in closed-canopy, mixed-coniferous forests at mid-elevations. Although the shared use of forests with these features placed the two species in close contact with one another, differences in geophysical position and habitat use may have minimized competition when the two species first became sympatric.

Our data indicating use of different types of nests and nest tree species by the two owls suggests the absence of significant competition for nest structures and perhaps nest sites. This perspective was based on data collected between 1988 and 1994, a period when Barred Owls appeared to be less common than at present. Indeed, Barred Owls now occur in many areas that several years previously supported only Spotted Owls (T. Fleming unpubl. data). Additionally, several Spotted Owl nests in our study area have been used by Barred Owls since 1994 (T. Fleming unpubl. data). Consequently, given the more generalist use of habitat by Barred Owls (Mazur and James 2000) compared to Spotted Owls, a future assessment of Barred Owl habitat use may indicate a different relationship between the two species.

ACKNOWLEDGMENTS

We thank Dale Herter, Michael Kane, Heather Murphy, Brian Ostwald, Stan Sovern, and Margy Taylor for directing us to Barred Owl nest sites or pair locations; many other biologists, acknowledged in earlier publications, for directing us to Spotted Owl nest sites; Leonard Brennan, for providing feedback on the analysis; and James Belthoff, Rob Bierregaard, Eric Forsman, and David Johnson for making constructive comments that improved the manuscript.

LITERATURE CITED

- AGEE, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, DC U.S.A.
- APFELBAUM, S.I. AND P. SEELBACH. 1983. Nest tree, habitat

- selection and productivity of seven North American raptor species based on the Cornell University nest record card program. *Raptor Res.* 17:97–113.
- BFNT, A.C. 1938. Life histories of North American birds of prey, part two. *U.S. Natl. Mus. Bull.* 170:96–99.
- BOSAKOWSKI, T., R. SPEISER, AND J. BENZINGER. 1987. Distribution, density, and habitat relationships of the Barred Owl in northern New Jersey. Pages 135–143 in R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre [Eds.], *Biology and conservation of northern forest owls*. USDA For. Serv., Gen. Tech. Rep. RM-142, Ft. Collins, CO U.S.A.
- BUCHANAN, J.B. AND L.L. IRWIN. 1998. Variation in Spotted Owl nest site characteristics within the eastern Cascade Mountains Province in Washington. *Northwest. Nat.* 79:33–40.
- , ———, AND E.L. MCCUTCHEN. 1993. Characteristics of Spotted Owl nest trees in the Wenatchee National Forest. *J. Raptor Res.* 27:1–7.
- , ———, AND ———. 1995. Spotted Owl nest site characteristics in the eastern Washington Cascades. *J. Wildl. Manage.* 59:301–310.
- CHAN, S.S., R.W. MCCREIGHT, J.D. WALSTAD, AND T.A. SPIES. 1986. Evaluating forest vegetative cover with computerized analysis of fisheye photographs. *For. Sci.* 32:1085–1091.
- CLINE, S.P., A.B. BERG, AND H.M. WIGHT. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *J. Wildl. Manage.* 44:773–786.
- COBB, D.F. 1988. Development of mixed western larch, lodgepole pine, Douglas-fir, grand fir stands in eastern Washington. M.S. thesis, Univ. Washington, Seattle, WA U.S.A.
- DARK, S.J., R.J. GUTIÉRREZ, AND G.I. GOULD, JR. 1998. The Barred Owl (*Strix varia*) invasion in California. *Auk* 115:50–56.
- DEVEREAUX, J.G. AND J.A. MOSHER. 1984. Breeding ecology of Barred Owls in the central Appalachians. *Raptor Res.* 18:49–58.
- FORSMAN, E.D., E.C. MESLOW, H.M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. *Wildl. Monogr.* 87.
- FALK, J.A. 1990. Landscape level raptor habitat associations in northwest Connecticut. M.S. thesis, Virginia Polytechnic Inst. and St. Univ., Blacksburg, VA U.S.A.
- FRANKLIN, J.F. AND C.T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv., Gen. Tech. Rep. PNW-8, Portland, OR U.S.A.
- GRANT, J. 1966. The Barred Owl in British Columbia. *Murrelet* 47:39–45.
- HAMER, T.E. 1988. Home range size of the Northern Barred Owl and Northern Spotted Owl in western Washington. M.S. thesis, Western Washington Univ., Bellingham, WA U.S.A.
- , E.D. FORSMAN, A.D. FUCHS, AND M.L. WALTERS. 1994. Hybridization between Barred and Spotted Owls. *Auk* 111:487–492.
- , D.L. HAYS, C.M. SENGER, AND E.D. FORSMAN. 2001. Diets of northern Barred Owls and northern Spotted Owls in an area of sympatry. *J. Raptor Res.* 35:221–227.
- HERSHEY, K. 1995. Characteristics of forests at Spotted Owl nest sites in the Pacific Northwest. M.S. thesis, Oregon State Univ., Corvallis, OR U.S.A.
- HERTER, D.R. AND L.L. HICKS. 2000. Barred Owl and Spotted Owl populations and habitat in the central Cascade Range of Washington. *J. Raptor Res.* 34:279–287.
- HOSMER, D.W. AND S. LEMESHOW. 1989. Applied logistic regression. John Wiley and Sons, New York, NY U.S.A.
- KELLY, E.G. 2001. The range expansion of northern Barred Owl: an evaluation of the impact on Spotted Owls. M.S. thesis, Oregon State Univ., Corvallis, OR U.S.A.
- , E.D. FORSMAN, AND R.G. ANTHONY. 2003. Are Barred Owls displacing Spotted Owls? *Condor* 105:45–53.
- LEDER, J.E. AND M.L. WALTERS. 1980. Nesting observations of the Barred Owl in western Washington. *Murrelet* 61:110–112.
- LEMMON, P.E. 1956. A spherical densiometer for estimating forest overstory density. *For. Sci.* 2:314–320.
- MAZUR, K.M. AND P.C. JAMES. 2000. Barred Owl (*Strix varia*). In A. Poole and F. Gill [Eds.], *The birds of North America*, No. 508. The Birds of North America, Inc., Philadelphia, PA U.S.A.
- MCGARIGAL, K. AND J.D. FRASER. 1984. The effect of forest stand age on owl distribution in southwestern Virginia. *J. Wildl. Manage.* 48:1393–1398.
- AND ———. 1985. Barred Owl responses to recorded vocalizations. *Condor* 87:552–553.
- MICKEY, J. AND S. GREENLAND. 1989. A study of the impact of confounder-selection criteria on effect estimation. *Am. J. Epidemiol.* 129:125–137.
- NELSON, R.W. 1983. Natural regulation of raptor populations. Pages 126–150 in D.S. Eastman, F.L. Bunnell, and J.M. Peek [Eds.], *Natural regulation of wildlife*. University of Idaho Press, Moscow, ID U.S.A.
- NEWTON, I. 1979. Population ecology of raptors. T. & A.D. Poyser, Berkhamsted, U.K.
- NICHOLLS, T.H. AND D.W. WARNER. 1972. Barred Owl habitat use as determined by radio-telemetry. *J. Wildl. Manage.* 36:213–224.
- PEARSON, R.R. AND K.B. LIVEZEY. 2003. Distribution, numbers, and site characteristics of Spotted Owls and Barred Owls in the Cascade Mountains of Washington. *J. Raptor Res.* 37:265–276.
- PEFFER, R.D. 2001. Small mammal habitat selection in east slope Cascade Mountain riparian and upland habitat. M.S. thesis, Eastern Washington Univ., Cheney, WA U.S.A.
- SNYDER, N.F.R. AND J.W. WILEY. 1976. Sexual size dimorphism in hawks and owls of North America. *Ornithol. Monogr.* 20.
- SOLLINS, P. 1982. Input and decay of coarse woody debris

- in coniferous stands in western Oregon and Washington. *Can. J. For. Res.* 12:18–28.
- TAYLOR, A.L. AND E.D. FORSMAN. 1976. Recent range extensions of the Barred Owl in western North America, including the first records for Oregon. *Condor* 78:560–561.
- USDI. 1990. Endangered and threatened wildlife and plants; determination of threatened status for the northern Spotted Owl. *Federal Reg.* 55:26114–26194.
- . 1992. Recovery plan for the northern Spotted Owl—final draft. U.S. Government Printing Office, Washington, DC U.S.A.
- YANNIELLI, L.C. 1991. Preferred habitat of northern Barred Owls in Litchfield County, Connecticut. *Conn Warbler* 11:12–20.
- ZAR, J.H. 1984. Biostatistical analysis, 2nd Ed. Prentice-Hall, Englewood Cliffs, NJ U.S.A.

Received 10 April 2003; accepted 10 May 2004

Associate Editor: James R. Belthoff

PRODUCTIVITY AND NEST-SITE CHARACTERISTICS OF GRAY HAWKS IN SOUTHERN ARIZONA

BRENT D. BIBLES¹ AND R. WILLIAM MANNAN

School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721 U.S.A.

ABSTRACT.—We studied Gray Hawks (*Asturina nitida*) nesting along the upper San Pedro River in southeastern Arizona from 1995–97. We identified 27 nesting areas with a mean of 24.3 nesting areas occupied per year. Productivity averaged 1.32 young per occupied nest. Number of successful nests and number of young produced per nest did not differ among years. Mean size of home range ($N = 10$ males), based on the 90% adaptive kernel method, was 59.2 ha (range = 21.4–91.2). Almost all Gray Hawk nests were located in large, dominant cottonwood trees (*Populus fremontii*). However, we doubt that Gray Hawks inherently prefer cottonwood trees over other species, but rather speculate that they use them because they are the only tall nest substrate currently available. The increase in Gray Hawks in southern Arizona during the past 30 yr was probably due to an increase in habitat. In the future, groundwater depletion may represent a risk to maintenance of Gray Hawk populations in southern Arizona.

KEY WORDS: *Gray Hawk; Asturina nitida; Arizona; home range; productivity; nest characteristics.*

PRODUCTIVIDAD Y CARACTERÍSTICAS DEL SITIO DEL NIDO DEL GAVILAN GRIS EN EL SUR DE ARIZONA

RESUMEN.—Estudiamos el gavián gris (*Asturina nitida*) anidando a lo largo de la cuenca alta del Río San Pedro en el sureste de Arizona desde 1995–97. Identificamos 27 áreas de anidación con una media de 24.3 áreas de anidación ocupadas por año. La productividad promedio fue de 1.32 juveniles por nido ocupado. El número de juveniles producidos por nido no difirió entre años. El tamaño de la media del rango de hogar ($N = 10$ machos), con base en el 90% del método adaptativo de kernel, fue de 59.2 ha (rango = 21.4–91.2). Casi todos los nidos del gavián gris estaban ubicados en grandes y dominantes árboles de álamo (*Populus fremontii*). Sin embargo dudamos que el gavián gris inherentemente prefiera los álamos a otra especie y especulamos que ellos los usan debido a que es el único árbol de gran porte dentro del substrato disponible. El aumento de gavián gris en el sur de Arizona durante los pasados 30 años probablemente se debe al aumento de hábitat adecuado. En el futuro, el agotamiento de las aguas subterráneas puede representar un riesgo para la sobrevivencia de las poblaciones del gavián gris en el sur de Arizona.

[Traducción de César Márquez]

There is little quantitative information on the behavior, habitat use, or productivity of Gray Hawks (*Asturina nitida*) during the breeding season. Glinski and Millsap (1987) and Glinski (1988) provide the only data on productivity of Gray Hawks in Arizona. Nesting habitat has not been quantified except for narrative descriptions of individual nest sites (Glinski 1988), and there is no information on home-range size or habitat use. However, Gray Hawks in Arizona are known to occupy riparian woodlands of mesquite (*Prosopis juliflora*) and hackberry (*Celtis reticulata*) that are ad-

jacent to stands of cottonwood (*Populus fremontii*) and willow (*Salix gooddingi*; Glinski 1988).

Currently, about 80 breeding pairs of Gray Hawks occur within the watersheds of the Santa Cruz and San Pedro rivers in southern Arizona (Glinski 1998). Cottonwood-willow and mesquite account for almost 93% of the riparian vegetation along these rivers (Hunter et al. 1987). Gray Hawks have recently increased in number within Arizona, probably due to an increase in habitat resulting from landscape changes that occurred over the past century (Glinski 1998). Effective management of Gray Hawk habitat requires knowledge of basic life history information. Therefore, we examined productivity, characteristics of nest sites and home ranges, and habitat use of Gray Hawks in Arizona.

¹ Present address: Colorado Division of Wildlife, 317 West Prospect Road, Fort Collins, CO 80526 U.S.A; e-mail address: brent.bibles@state.co.us

STUDY AREA

We studied Gray Hawks breeding along the San Pedro River in southeastern Arizona from 1995–97. The boundaries of the San Pedro Riparian National Conservation Area (SPRNCA), administered by the Bureau of Land Management, defined our study area. The SPRNCA encompasses about 23 500 ha along 64 km of perennial and intermittent river at elevations ranging from 1125–1280 m.

METHODS

We conducted fieldwork from early April–July of each year. We located nests of Gray Hawks by intensively searching cottonwood forests along the river early in the breeding season. Gray Hawk nests are relatively easy to locate because the hawks are vocal prior to incubation, and give alarm calls when humans enter the nest area. After a vocal pair was located, we searched all large trees nearby for nest structures. We considered a site occupied if a pair was present in the area performing behaviors consistent with nesting activities (e.g., vocalizations), regardless of whether a nest was located. We revisited occupied sites at least four times throughout the breeding season to determine productivity. A nest was considered successful if nestlings were observed within 2 wk of the normal fledging age of 42 d (i.e., >28-d-old; Glinski 1988). We climbed the nest tree, usually ≤ 2 wk before the nestlings fledged, to determine the number of young produced. We counted and determined the gender of nestlings based on diameter of the tarsus (Hull and Bloom 2001), and fitted them with U.S. Geological Survey bands. If we could not safely climb a nest tree, we counted nestlings from the ground. At least two visits were made to these nests during the late-nestling stage to confirm counts.

Each year, we determined the number of sites at which nesting was attempted, the number of sites that produced young successfully (i.e., young within 2 wk of fledging age), and the number of young produced at each site. We used the log-likelihood chi-square test (Sokal and Rohlf 1981) to compare the number of successful nests among years, and the Kruskal-Wallis test to compare the number of young produced among years (Gibbons 1985).

We followed radio-tagged, breeding, male Gray Hawks to develop home-range estimates. We used a dho-gaza set, with a live Great Horned Owl (*Bubo virginianus*) as a lure (Bloom 1987), to capture hawks. We attempted to capture hawks at sites representing all sections of the study area. We used epoxy and dental floss to attach radiotransmitters (Holohil Systems PD-2 transmitters, Carp, Ontario, Canada) to the central rectrix that exhibited the least wear (Dunstan 1973). Transmitters weighed 3.8 g, <1% of the mass of adult males.

We followed radio-tagged males ca. weekly during 4–8 hr sessions with the aid of a Telonics TR-4 receiver and RA-14 “H” antenna (Telonics, Mesa, AZ). We terminated observation sessions if it appeared that the hawk was changing its behavior as the result of our activities. We used homing (White and Garrott 1990) to relocate birds at hourly intervals during each session. We mapped locations of trees upon which hawks were perched on transparent overlays of aerial photos. We only used locations when we had a high degree of confidence that the bird

was within 30 m of the mapped location. This level of accuracy was determined by visual or auditory confirmation of the bird’s location, or by partially circling the location and noting the change in direction of the radio signal.

We used a geographic information system (Arc/Info and ArcView 3.1, Environmental Systems Research Institute, Inc., Redlands, CA) to obtain coordinates of bird locations. We digitally scanned the aerial photos used for field mapping and registered the scanned images to existing digital maps of the study area. We then digitized hawk locations using the digital photos as a reference. We used the 90% adaptive kernel (AK) and minimum convex polygon (MCP) methods (RANGES V, Institute for Terrestrial Ecology, London, U.K.) to calculate boundaries of home ranges. We calculated AK home ranges using a 40×40 -m grid, and applied a smoothing factor determined by least squares cross validation. We calculated home ranges only when we obtained ≥ 30 observations on a hawk (Seaman et al. 1999).

We measured or calculated 14 structural features at each nest site. We used a clinometer to measure height of the nest, the nest tree, and adjacent forest. Height of the adjacent forest was determined by measuring the heights of the four nearest dominant trees within 100 m of the nest tree. We averaged these heights to estimate the adjacent forest height. We used a convex spherical densiometer (Lemmon 1957) to estimate cover. Within the nest tree, we estimated nest cover by averaging densiometer readings from two locations directly on top of the nest structure. From the ground, we estimated canopy cover by averaging densiometer readings from directly under the nest and at points 10 m in each cardinal direction from the point directly under the nest. We used a diameter tape to measure diameter at breast height (DBH) of the nest tree. We used a compass to determine the directional quadrant (northeast, northwest, southeast, southwest) of the tree in which the nest was located, relative to the main stem. At the nest, we measured the maximum and minimum widths of the nest structure, depth of the nest from top of rim to deepest point, and depth of cup from top of rim to deepest point. We recorded species of the nest tree. In addition, two variables were calculated, nest position and nest-tree dominance. Nest position was the nest height expressed as the percent of the nest-tree height. Nest-tree dominance is the nest-tree height divided by the adjacent forest height. Dominance values below one indicate the tree is shorter than the surrounding trees (i.e., subordinate), and values greater than one indicate the tree is taller than the surrounding trees (i.e., dominant).

We used the log-likelihood chi-square test (Manly et al. 1993) to examine whether nests were uniformly distributed among quadrants. We used a *t*-test to compare vertical cover at the nest to ground-based cover in the nest-tree vicinity. We used the arcsine transformation (Sokal and Rohlf 1981) to transform cover percentages. We used a *t*-test to compare nest tree height with adjacent forest height. We transformed tree heights using the natural-log transformation because they were not normally distributed.

Table 1. Number of occupied nest areas, number of nest areas with pairs that produced young successfully, and number of young produced at Gray Hawk nests at the San Pedro National Conservation Area, Cochise County, AZ, 1995–97.

	1995	1996	1997	TOTAL
Occupied ^a	25	23	25	73
Successful ^b	14	15	19	48
Young produced ^c	28	29	39	96

^a A nesting area at which two adult birds were located and observed exhibiting behaviors typical of nesting (e.g., vocalizations), regardless of whether a nest structure was located.
^b A nesting area at which nestlings were present within 2 wk of normal fledging age, i.e., >28-d old.
^c The number of young counted at successful nests (see Methods).

RESULTS

We identified 27 breeding territories that resulted in 73 nesting attempts during the 3 yr of this study (Table 1). Number of successful breeding pairs (log-likelihood $\chi^2_2 = 2.257$, $P = 0.3235$) did not differ among years, with a mean of 16 successful pairs per year (range = 14–19). Individual breeding sites exhibited variation in number of years occupied and successful (Table 2).

Productivity averaged 1.32 young per occupied site during the 3 yr of the study (range = 1.12–1.56). Number of young produced (Kruskal-Wallis, $\chi^2_2 = 2.3096$, $P = 0.3151$) did not differ among years. Number of young per successful site was 2.0 over the 3 yr (range = 1.93–2.05). Individual sites produced 0 to 8 young over the 3-yr period ($\bar{x} = 3.56$).

Gray Hawks used 52 nest structures during the 3 yr of the study, with a mean of 1.38 nests used per nesting area. Four nests (7.7%) were used during all 3 yr. Twelve nests (23.1%) were used during 2 yr. The remaining 36 nests (69.2%) were used only once. The breeding attempt at one nesting area failed prior to completion of a nest.

Breeding hawks at territories in which the pair failed during the previous year tended to use new nest structures the following year more often than hawks at sites in which the pair was successful the previous year (Fisher’s exact test, $P = 0.0644$). We excluded territories that were unoccupied the following year from the above analysis.

We determined home ranges for 10 breeding males. Estimated home ranges were based on a mean of 52 locations (range = 36–65). Size of

Table 2. Number of Gray Hawk nest areas at which pairs were successful according to number of years of the study during which they were successful at the San Pedro National Conservation Area, Cochise County, AZ, 1995–97. A nesting area was considered successful when nestlings were present within 2 wk of normal fledging age (>28-d old).

	SUCCESSFUL ALL SITES ^a	SUCCESSFUL 3-YR SITES ^b
All years	9	9
2 of 3 yr	7	6
1 of 3 yr	7	5
0 of 3 yr	4	1
Total	27	21

^a The number of nest areas, out of all identified nesting areas, at which pairs were successful during 0, 1, 2, or 3 yr.
^b The number of nest areas, out of the 21 areas at which pairs were present (i.e., occupied sites) during all 3 yr of the study, at which pairs were successful during 0, 1, 2, or 3 yr.

home ranges based on the AK method averaged 59.2 ha (range = 21.4–91.2 ha). Size of home ranges based on the MCP method averaged 90.3 ha (range = 47.6–179.5 ha).

Fifty of the 52 Gray Hawk nests we located were in cottonwoods. The remaining two nests, both located within the same nesting area, were in willow trees. Vertical cover over nests was significantly higher than vertical cover measured from the ground near the nest tree ($t_{48} = -2.863$, $P = 0.0062$; Table 3). Nest trees were significantly higher than the surrounding trees ($t_{50} = -3.012$, $P = 0.0041$).

DISCUSSION

The productivity we recorded (1.32 young/occupied site) is slightly higher than the 1.18 young/occupied site observed in Arizona from 1973–76 (Glinski 1988). However, the range of productivity during our study falls within that observed during the 1970s (0.71–1.67 young/occupied site; Glinski and Millsap 1987). Therefore, our data do not likely represent an increase in productivity of the Gray Hawk population in Arizona. The rate of productivity we observed is consistent with observed rates for other medium-sized raptors (Newton 1979).

Gray Hawks have small home ranges and adjacent nests may be in close proximity. The mean home range (90.3 ha; MCP method) is about half the 170 ha observed for males of the similar-sized Red-shouldered Hawk (*Buteo lineatus*) in California

Table 3. Summary statistics for 12 variables measured at Gray Hawk nest sites at San Pedro National Conservation Area, Cochise County, AZ, 1995–97. Some measurements could not be obtained at all nests.

FEATURE	\bar{x}	SE	N	95% CI	RANGE
Nest height (m)	19.2	0.80	26	[17.6, 20.9]	14.2–31.5
Tree height (m)	30.0	1.31	26	[27.3, 32.7]	23.0–45.0
Adjacent forest height (m)	25.0	1.17	26	[22.6, 27.4]	13–43.5
Nest position % ^a	64.9	2.01	26	[60.8, 69.1]	50.0–83.3
Dominance ^b	1.23	0.05	26	[1.12, 1.34]	0.90–1.96
Canopy cover (%)	86.8	1.92	26	[82.8, 90.7]	55–98
DBH (cm)	92.5	7.28	26	[77.5, 107.5]	48.5–181.0
Nest diameter (max cm)	50.7	1.82	26	[47.0, 54.4]	23–66
Nest diameter (min cm)	40.3	1.70	25	[36.8, 43.8]	18–53
Nest depth (cm)	26.4	1.41	26	[23.5, 29.3]	13–40
Cup depth (cm)	2.7	0.42	26	[1.8, 3.5]	0–7
Nest cover (%)	92.8	1.87	24	[88.9, 96.6]	63–100

^a Vertical location of nest in tree (nest height \times 100/nest tree height).

^b Nest tree dominance (nest tree height/adjacent forest height).

(Bloom et al. 1993). It is possible that Gray Hawks have smaller breeding home ranges than any other North American buteonine raptor.

We found that Gray Hawks usually built nests in dominant cottonwoods. Nests were placed in the upper half of cottonwoods, usually away from the main stem of the tree. Gray Hawks are known to be associated with cottonwood forests and mesquite woodlands in the northern portion of their range (Glinski 1988). Mesquite woodlands have been assumed to function as the primary foraging areas, with cottonwood forests being used primarily for nesting (Stensrude 1965, Glinski 1988). Historically, Gray Hawks were reported to nest >9-m high in mesquites (Bent 1937). Few, if any, mesquite trees of this size remain in Arizona. Furthermore, few trees other than cottonwoods remaining along riparian areas in southern Arizona are this tall. Gray Hawks probably select the most dominant trees in an area for nesting, regardless of species. Eventually Gray Hawks may begin nesting in mesquite trees as these grow to heights that are suitable for nesting.

The number of breeding Gray Hawks has increased along the upper San Pedro River during the last 25 yr, and in Arizona as a whole. In the early–mid 1970s, statewide there were 39 known nesting areas, including some that were not producing young or were occupied by a single adult (Porter and White 1977). There are now over 80 known nesting areas (Glinski 1998). During this study (1995–97), 23–25 nest territories were occupied along this 64 km of river. Gray Hawks were

first recorded nesting on the San Pedro River in 1964 (Glinski and Millsap 1987). In 1977, 16 sites were known along the entire river, 11 within our study area (Glinski and Millsap 1987). In 1985, 20 territories were known for the entire river, again with 11 nests within our study area (Glinski and Millsap 1987). The increasing number of breeding Gray Hawks along the San Pedro River probably was the result of an increase in habitat for this species in this area. Prior to 1900, vegetation along the river consisted of extensive areas of cienega, with some areas of cottonwood forest and mesquite. Woodcutting heavily impacted the cottonwood and mesquite forests during the late 1800s (Tellman et al. 1997). By 1920, mesquite had replaced most of the cienegas along the river (Tellman et al. 1997). The number of Gray Hawks has probably increased as areas of mesquite along the river have matured into extensive woodlands providing increased foraging habitat for nesting Gray Hawks.

However, continued growth of trees within mesquite woodlands, as well as presence of cottonwood forests along the San Pedro River depends on maintenance of the existing water table along the river (Tellman et al. 1997). Depletion of groundwater and human development already has resulted in the loss of much of the mesquite woodlands and cottonwood forests along the nearby Santa Cruz River (Tellman et al. 1997), with many areas that had significant numbers of Gray Hawks no longer providing habitat for this species. For example, Bendire (1882, 1892) described several

Gray Hawk nests along Rillito Creek in Tucson, an area that now both dewatered and urbanized, and reported that the Gray Hawk was considered common in the Tucson area. Swarth (1905) described several nests in the mesquite forest around the San Xavier mission south of Tucson that contained trees as high as 18 m. This forest no longer exists. Gray Hawks were absent from this area by 1948, when the Santa Cruz River was no longer a permanent stream in Arizona (Phillips et al. 1964). Historically, these woodlands were the center of the Gray Hawk population in Arizona (Glinski 1988). Maintenance of adequate levels of groundwater may be the most important requirement for ensuring long-term presence of breeding Gray Hawks along the San Pedro River, and in Arizona, by ensuring continued presence of the cottonwood and mesquite forests that provide habitat.

ACKNOWLEDGMENTS

We would like to thank the many people who helped us gather field data including Clint Boal, Laurel Christoferson, Adam Duerr, Tracy Estabrook, Peter Gaede, Nick Heatwole, Joe Hoscheidt, and Rick Spaulding. In addition, this project could not have been completed without the cooperation and support of the Bureau of Land Management's San Pedro Project Office, especially Dave Kreuper and Jack Whetstone. This manuscript benefited from the reviews of Richard Glinski, Brian Millsap, and an anonymous reviewer.

LITERATURE CITED

- BENDIRE, C.E. 1882. Mexican goshawk. *Ornithol. and Oologist* 6:87–88.
- . 1892. Life histories of North American birds, with special reference to their breeding and eggs. *Spec. Publ. U.S. Natl. Mus.* 1:251–255.
- BENT, A.C. 1937. Life histories of North American birds of prey, part 1. *U.S. Natl. Mus. Bull.* 167.
- BLOOM, P.H. 1987. Capturing and handling raptors. Pages 99–123 in B.A. Millsap, K.W. Cline, B.G. Pendleton, and D.A. Bird [Eds.], *Raptor management techniques manual*, National Wildlife Federation, Washington, DC U.S.A.
- , M.D. McCrory, and M.J. Gibson. 1993. Red-shouldered Hawk home-range and habitat use in southern California. *J. Wildl. Manage.* 57:258–265.
- DUNSTAN, T.C. 1973. A tail feather package for radio-tagging raptorial birds. *Inland Bird-Banding News* 45:3–6.
- GIBBONS, J.D. 1985. Nonparametric methods for quantitative analysis. American Sciences Press, Columbus, OH U.S.A.
- GLINSKI, R.L. 1988. Gray Hawk. Pages 83–86 in R.L. Glinski, B.G. Pendleton, M.B. Moss, M.N. LeFranc, Jr., B.A. Millsap, and S.W. Hoffman [Eds.], *Proceedings of the southwest raptor management symposium and workshop*. National Wildlife Federation, Washington, DC U.S.A.
- . 1998. Gray Hawk. Pages 82–85 in R.L. Glinski [Ed.], *The raptors of Arizona*. Univ. of Arizona Press, Tucson, AZ U.S.A.
- AND B.A. MILLSAP. 1987. Status of the Sonora Gray Hawk *Buteo nitidus maximus* (van Rossem 1930). USDI Fish and Wildl. Serv. Unpubl. report, Albuquerque, NM U.S.A.
- HULL, B. AND P. BLOOM. 2001. The North American banders' manual for raptor banding techniques. North American Banding Council, Point Reyes Station, CA U.S.A.
- HUNTER, W.C., R.D. OHMART, AND B.W. ANDERSON. 1987. Status of breeding riparian-obligate birds in southwestern riverine systems. *West. Birds* 18:10–18.
- LEMMON, P.E. 1957. A new instrument for measuring forest over-story density. *J. For.* 55:667–669.
- MANLY, B., L. McDONALD, AND D. THOMAS. 1993. Resource selection by animals. Chapman & Hall, New York, NY U.S.A.
- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.
- PHILLIPS, A.R., J. MARSHALL, AND G. MONSON. 1964. The birds of Arizona. Univ. Arizona Press, Tucson, AZ U.S.A.
- PORTER, R.D. AND C.M. WHITE. 1977. Status of some rare and lesser known hawks in western United States. Pages 39–57 in R.D. Chancellor [Ed.], *Report of proceedings: world conference on birds of prey*, Vienna, 1–3 October 1975. Int. Counc. Bird Preserv., London, U.K.
- SEAMAN, D.E., J.J. MILLSPAUGH, B.J. KERNOHAN, G.C. BRUNDIGE, K.J. RAEDEKE, AND R.A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *J. Wildl. Manage.* 63:739–747.
- SOKAL, R.R. AND F.J. ROHLF. 1981. Biometry. W.H. Freeman and Company, New York, NY U.S.A.
- STENSRUDE, C. 1965. Observations on a pair of Gray Hawks in southern Arizona. *Condor* 67:319–321.
- SWARTH, H.S. 1905. Summer birds of the Papago Indian Reservation and of the Santa Rita Mountains, Arizona. *Condor* 7:22–27.
- TELLMAN, B., R. YARDE, AND M.G. WALLACE. 1997. Arizona's changing rivers: how people have affected the rivers. Water Resources Research Center Issue Paper 19, Univ. of Arizona, Tucson, AZ U.S.A.
- WHITE, G.C. AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc, New York, NY U.S.A.

Received 15 October 2002; accepted 11 May 2004
Associate Editor: Marco Restani

JUVENILE GROUSE IN THE DIET OF SOME RAPTORS

VITALI REIF¹ AND RISTO TORNBERG

Department of Biology, University of Oulu, P.O. Box 3000, FIN-90014 Oulu, Finland

KAUKO HUHTALA

Tehtaanpuistokatu 3, FIN-85310 Sievi, Finland

ABSTRACT.—Grouse (e.g., *Tetrao*) constitute a significant part of the diet for some raptors. Especially grouse chicks are important for several avian predators including species that normally prey upon small mammals. To evaluate the impact of avian predation on grouse, we need to know which raptors are hunting which species and when juvenile grouse suffer from the heaviest predation. Because grouse chicks are difficult to identify in prey samples based on morphological characteristics, we made an attempt to address this problem by measuring the humerus size of grouse chicks found in prey remains of Northern Goshawks (*Accipiter gentilis*), Eurasian Sparrowhawks (*Accipiter nisus*), Common Buzzards (*Buteo buteo*), and Northern Harriers (*Circus cyaneus*). Then, we plotted humerus sizes from prey remains against growth curves of chicks of Capercaillie (*Tetrao urogallus*), Black Grouse (*Tetrao tetrix*), Willow Grouse (*Lagopus lagopus*), and Hazel Grouse (*Bonasa bonasia*). We found that the size of grouse chicks in the diet was best explained by the mass of raptors, but not the fledging date of their young. Ranges of grouse size in the raptor diets were overlapping, suggesting that all four raptor species hunt grouse chicks at about the same dates. Pressure of the avian predator assemblage on juvenile grouse does not appear to be uniform; smaller grouse species suffer from heavier predation during a longer period than larger grouse.

KEY WORDS: Northern Goshawk; *Accipiter gentilis*; Eurasian Sparrowhawk; *Accipiter nisus*; Common Buzzard; *Buteo buteo*; Northern Harrier; *Circus cyaneus*; grouse; predation; Finland.

LAGOPODOS JUVENILES EN LA DIETA DE ALGUNAS AVES RAPACES

RESUMEN.—El lagopodo (*Tetrao*) constituye una parte significativa en la dieta de algunas rapaces, en especial los pichones del lagopodo son importantes para muchos depredadores de aves incluyendo especies que normalmente se alimentan de pequeños mamíferos. Para evaluar el impacto de la depredación sobre el lagopodo, necesitamos saber cuales rapaces están cazado a cuales especies y cuando los juveniles del lagopodo se ven afectados por la mayor depredación. Debido a que los pichones de lagopodo son difíciles de identificar en los restos de presas basados en características morfológicas, hicimos un ensayo para resolver el problema mediante la medición del tamaño del numero de los pichones de lagopodo encontrados en los restos del azor (*Accipiter gentilis*), el gavilán euroasiático (*Accipiter nisus*), el ratonero común (*Buteo buteo*), y el aguilucho norteño (*Circus cyaneus*). Posteriormente planteamos el tamaño del numero de los restos de presas versus las curvas de crecimiento de, los pichones de *Tetrao urogallus*, *Tetrao tetrix*, *Lagopus lagopus*, y *Bonasa bonasia*. Encontramos que el tamaño de los pichones de lagopodo en la dieta se entiende mejor a partir de la masa de las rapaces y por la fecha del emplumamiento de los juveniles. Los rangos del tamaño del lagopodo en la dieta de las rapaces se superpusieron, lo cual sugiere que las cuatro especies de rapaces cazan pichones aproximadamente en las mismas fechas. La presión del ensamblaje de los depredadores aviares en los juveniles de lagopodo, es aparentemente uniforme; las especies menores de lagopodo sufren una mayor depredación durante un periodo mas largo que las especies de lagopodo de mayor tamaño.

[Traducción de César Márquez]

The tetraonids constitute a significant portion in the diet of some birds of prey. For some of them

(e.g., Northern Goshawk [*Accipiter gentilis*], Gyrfalcon [*Falco rusticolus*], Golden Eagle [*Aquila chrysaetos*]) small game are commonly-taken prey (Huhtala et al. 1996, Tornberg 1997, Sulkava et al. 1998, Nielsen 1999). For others, such as those that feed

¹ E-mail address: vitali.reif@oulu.fi

mainly on small mammals (e.g., Common Buzzard [*Buteo buteo*], Northern Harrier [*Circus cyaneus*], Eurasian Eagle-Owl [*Bubo bubo*], Ural Owl [*Strix uralensis*]), the tetraonids may become an alternative prey in poor vole (*Microtus* spp.) years (Angelstam et al. 1984, Korpimäki et al. 1990, Redpath and Thirgood 1999, Reif et al. 2001), when they can be an important source of food to support breeding.

Depending on their size and hunting capacity, raptors kill both juvenile and adult grouse (e.g., P. Sulkava 1964, S. Sulkava 1964, Tornberg 1997, Sulkava et al. 1998, Reif et al. 2001). There are few quantitative studies regarding raptor predation on grouse chicks (S. Sulkava 1964, Höglund 1964, Grønnesby and Nygård 2000, Thirgood et al. 2000), in part because the latter are difficult to identify to the species level in prey remains. Five grouse species (Capercaillie [*Tetrao urogallus*], Black Grouse [*Tetrao tetrix*], Hazel Grouse [*Bonasa bonasia*], Willow Grouse [*Lagopus lagopus*], and Ptarmigan [*Lagopus mutus*]) found in Fennoscandia come in a variety of sizes from 350 g (Hazel Grouse) to 4000 g (Capercaillie cock). The growth rate of their chicks varies correspondingly (e.g., Semenov-Tian-Shansky 1959, Lindén 1981, Klaus et al. 1990). Large raptor species might prey relatively little on grouse chicks generally (e.g., Golden Eagle; Sulkava et al. 1998) or mainly on chicks of large grouse species (e.g., Northern Goshawk; S. Sulkava 1964, Tornberg 2001). However, the latter soon escape predation of small raptor species, such as Eurasian Sparrowhawks (*Accipiter nisus*) and the Northern Harriers.

To assess the predation impact of the whole community of raptors on different grouse species, we need to know the variation in the size of grouse chicks in the diet of different avian predators. In our study area, goshawks, sparrowhawks, buzzards, and harriers hunt small game on a regular basis. The aim of this study was to determine how these predators partition this common food resource—grouse chicks. We used a large existing prey-remains collection of the Zoological Museum, University of Oulu, and published data. We expected that the selection of juvenile grouse by these predators would depend: (1) on the size of the raptor that generally accords with the size of the prey and, (2) because of rapid growth of grouse chicks and temporal variations in breeding times of the raptors, on the date of capture. In addition, we attempted to assess which species of grouse are most vulnerable to raptor predation and during which

time period this occurred. We compared the appearance and the growth of grouse chicks in the field with the size of juvenile grouse in the diet of these four avian predators during the late nesting period in July, when most prey remains accumulate in raptor nests.

MATERIAL AND METHODS

The prey material was collected in Finland in the following areas: Oulu (goshawk, sparrowhawk, harrier), Kuusamo (goshawk), and Central Ostrobothnia (harrier, buzzard). Most of the material was collected in Oulu (65°00'N, 25°30'E) and Central Ostrobothnia (64°00'N, 24°00'E). These areas represent coastal lowland with many small rivers and lakes. Roughly 67% of the area is covered by mosaic of spruce (*Picea abies*) and pine forests (*Pinus sylvestris*) mixed with birch (*Betula pubescens*). About half of the forested area includes bogs, a large number of them being drained. Cultivated areas with settlements are situated mainly in river valleys. Kuusamo (66°00'N, 29°00'E) is a rolling highland area, the highest hilltops reaching 450 m above the sea level. Area is also characterized by large lakes. Coniferous forests comprise more than 70% of the area, with fewer bogs than the previous area. Due to lower population density, the area cultivated is less in Kuusamo than in the Oulu-Ostrobothnia area.

The prey remains analyzed were collected during different years between 1966–2003 (Table 1). Prey remains and pellets were collected from the nests after fledging once a year. Prey remains for goshawks were collected also from the area surrounding the nest during the post-fledging period (after the young leave the nest, but stay in the nesting area). The total number of collected samples varied among the species as follows: goshawks, 32 (and 14 from nest areas); buzzards, 74; sparrowhawks, 14; harriers, 7. We assumed that most collected prey remains were accumulated in the nests shortly before fledging, because females often clean their nests when they rear small chicks (Dement'ev and Gladkov 1951, pers. observ.).

To determine the size of grouse chicks in the diet we measured the length of humeri. The humeri of juvenile grouse were distinguished from the adults' by the degree of ossification. There are four grouse species present in the study area: Willow Grouse, Black Grouse, Capercaillie, and Hazel Grouse. However, the bones of grouse chicks were not sorted by species because they could not be identified with certainty. When two opposite humeri of the same size were found, we counted this material as one animal.

We compared the size of grouse chicks (expressed in humerus length) found in the diet of each raptor at the end of its nestling period (and post-fledging period for the goshawk) with sizes of grouse chicks of different species derived from growth curves (Fig. 1). Given the scarcity of grouse remains in many nests, we were not able to consider each nest as a unit for analysis; therefore, each grouse chick was considered an experimental unit instead. Fledging dates of raptors were calculated by adding the length of the nestling periods (Cramp and Simmons 1980) to hatching dates. We calculated hatching

Table 1. Juvenile grouse in the prey-remain collections at raptor nests in Finland.

SPECIES	NO. OF SAMPLES WITH JUV. GROUSE HUMERI	TOTAL NO. OF JUV. GROUSE HUMERI	MEAN HUMERI IN A SAMPLE	SE	YEARS OF COLLECTION
Northern Goshawk (nest)	21	40	1.9	0.18	1967, 1970–73, 1975, 1978, 1980, 1984, 1987–90
Northern Goshawk (nest area)	9	18	2.0	0.44	1994–96, 1998, 2001
Common Buzzard (nest)	14	22	1.6	0.29	1997, 1984, 1986–91, 1996
Eurasian Sparrowhawk (nest)	13	22	1.7	0.16	1985, 1988–91, 1995
Northern Harrier (nest)	7	19	2.7	0.62	1966, 1971, 1976–77

dates by estimating the age of chicks from wing lengths based measurement data on known-aged birds and a nonlinear-regression model: $y = x^3 - 0.002x^2 + 0.325x - 0.534$ (Törnberg unpubl. data). The wing-growth pattern has been found to be fairly similar for raptors weighing around 1 kg (Kenward et al. 2000). For the sparrowhawk, we used a growth curve developed by Moss (1979). We found the following hatching dates (in Julian days) for different birds of prey: goshawk, 154.18 ± 0.67 (SE; 2 June; $N = 146$); buzzard, 151.94 ± 0.44 (31 May; $N = 282$); harrier, 167.77 ± 1.01 (16 June; $N = 52$); sparrowhawk, 172.58 ± 0.52 (21 June; $N = 90$).

The growth patterns of grouse chicks (in terms of body mass) were taken from Lindén (1981) for Capercaillie, from Klaus et al. (1990) for Black Grouse, and from Semenov-Tian-Shansky (1959) for Hazel and Willow grouse. For the latter two species, the growth patterns were given with calendar dates without exact age reference; therefore, we aged those Hazel and Willow grouse with given masses according to our own observations and by comparing their mass/age ratios to that of Black Grouse. The body mass of chicks was converted into humerus length

using a curve calculated from material of the Zoological Museum, University of Oulu (Power model: $y = 4.8104x^{0.4234}$, $r^2 = 0.962$, $N = 16$, $P < 0.001$; Fig. 1). Given the lack of data for newly-hatched chicks, the growth curves start at the age of 10 d. The hatching time of grouse was obtained from literature (von Haartman et al. 1963–72, Lindén 1983, Marjakangas and Törmälä 1997), P. Helle (pers. comm.), and our own observations. Variation of hatching dates is available only for Black Grouse studied by radiotelemetry in Kainuu, 200 km east of Oulu (Marjakangas and Törmälä 1997, Marjakangas unpubl. data). The mean hatching date for 126 Black Grouse broods in 1991–95 was 165.8 ± 0.421 Julian days (14 June). We assumed that the correspondent time span of hatching period was similar for all other grouse species.

Because sample sizes differed among the raptor species, and were relatively small for all but goshawks, only variations in mean grouse size in the diet (Fig. 2) were tested statistically. Correspondence of the size of juvenile grouse in the diet to the size of different grouse species in the wild was analyzed only visually on the graphs (Figs. 2–4). Capability of the raptors to kill juvenile grouse of different size (i.e., the whole size range; Fig. 4) was derived based on single specimens of maximal and minimal size. In order to find the time period when juvenile grouse suffer from the heaviest predation, we plotted dimension zones on graphs that corresponded to the full ranges of grouse size taken in raptor diets. On the time scale, these “predation zones” begin at the point when any of the grouse species reaches the minimal size hunted by the raptor (Figs. 3a–d). The growth curves of grouse species plotted over the zones indicate when grouse grow in and out of the “predation zones.” This analysis was done based on the assumption that the full range of grouse size in raptor diet does not change through the summer. Because all these raptors are capable of killing even adults of the smallest grouse, the “predation zones” are not limited on the right side (toward the end of the summer). These zones, when plotted together indicate an overlapping area in which the size of grouse chicks makes them vulnerable to predation by all four raptor species (Fig. 4).

RESULTS

The size of juvenile grouse (expressed as humerus length) found in the raptor nests differed

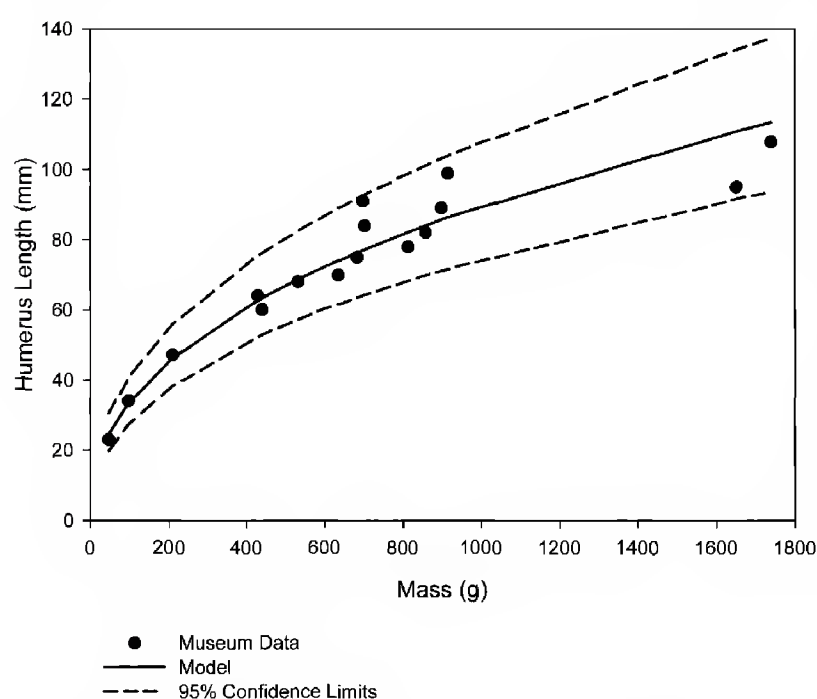


Figure 1. Model employed to estimate juvenile grouse humerus size based on mass.

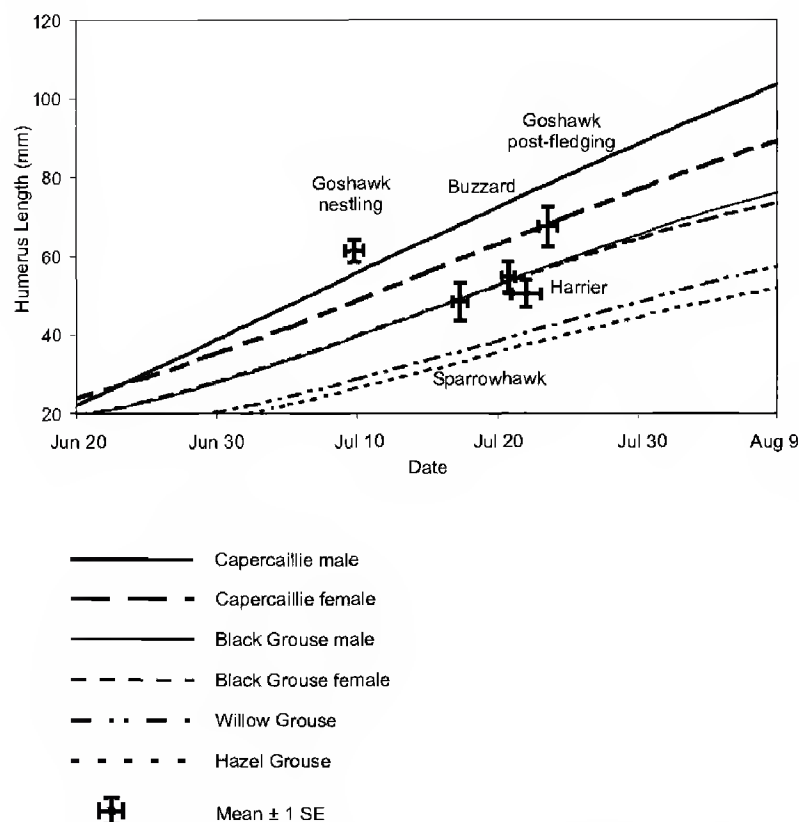


Figure 2. Mean size of humeri of grouse chicks in the diet of raptors in relation to fledging dates of raptors. The growth curves of humeri of different grouse species are also presented (see Materials and Methods). Crosses show relationship of fledgling periods (horizontal bars) to humeri lengths of grouse remains (vertical bars). For Northern Goshawks two crosses are shown; (1) late nestling period (about fledgling date) and (2) data collected during the post-fledging period.

significantly among the species (one-way ANOVA, $F = 11.64$, $P < 0.001$). The grouse chicks in the prey remains of goshawks were larger than those from the nests of other raptors (Tukey test: sparrowhawks, $P < 0.001$; buzzards, $P < 0.05$; harriers, $P < 0.001$; Fig. 2, Table 2). The largest grouse chicks were also found among the goshawk prey, whereas sparrowhawks killed the smallest grouse (Fig. 2, Table 2). During the post-fledging period, the goshawks killed larger grouse chicks (\bar{x} length = 68 mm) than during the late-nestling period (62 mm; $t = -2.26$, $df = 56$, $P < 0.05$). Using stepwise-linear regression, we found that the size of the grouse chicks in the diet was explained by the mass of the raptor female ($F = 14.5$, $B = 0.0116$, $R^2 = 0.26$, $P < 0.001$), but not by the date of fledging or mean mass of the male.

We plotted variations of grouse size in the raptor diets against the growth curves of grouse according to the time when the prey remains were presumably accumulated (Figs. 3a–d). This enables visual analysis of the correspondence between the grouse size in the diet and the size of chicks of different

grouse species in the wild at the same time. The smallest chick (the minimal value of humerus size) was found in the sparrowhawk nests (Fig. 3b). According to the regression model, this chick's mass was 84 g, which corresponds to the age of about 10 d for Capercaillie, 20 d for Black Grouse, 25 d for Willow Grouse and Hazel Grouse. Grouse chicks taken by goshawks in the nestling period were clearly larger than chicks of any grouse species (Fig. 2). Sparrowhawks delivered chicks to the nest around the size of the Black Grouse, which were larger than Willow and Hazel grouse chicks but smaller than female Capercaillie chicks. Chicks killed by buzzards were closest to the size of Black Grouse chicks, but were smaller than female chicks of Capercaillie and larger than Willow Grouse chicks. The size of grouse chicks taken by harriers was close to the size of Black Grouse, and larger than that of Willow Grouse chicks. Finally, grouse chicks found in goshawk diet during the post-fledging period were about the size of female Capercaillie, but smaller than male chicks of Capercaillie and larger than Black Grouse chicks (Fig. 2).

The lowest size limit of the “four-species predation zone” (i.e., when grouse chicks were hunted by all the raptor species) was 45-mm humerus, which was limited by the goshawk's diet (Fig. 4), and corresponds to the age of about 20 d for Capercaillie, 30 d for Black Grouse, 35 d for Willow Grouse, and 40 d for Hazel Grouse. The upper size boundary of the zone (65 mm humerus) is limited by the harrier's diet and ca. corresponds to 30-d-old males and 35-d-old females of Capercaillie, 45-d-old Black Grouse, 65-d-old Willow Grouse and older than 80-d (adult-size) Hazel Grouse.

DISCUSSION

The size of grouse chicks in prey remains of raptor species differed significantly. However, variances of sizes within each class overlap considerably (Fig. 4). Thus, we were not able to determine exactly which grouse species each raptor was taking. We found that the goshawk took relatively larger grouse chicks than sparrowhawks (Fig. 2). This was clearly related to the size of the raptors (Table 2). In the diet of goshawks, grouse chicks comprised 7% in June, 24% in July, and 41% in August by number (Tornberg 1997). This can be explained by the growth of the different grouse species, which makes them more profitable as a food item toward late summer. In the beginning of July, only the Capercaillie chicks seem to reach the size that

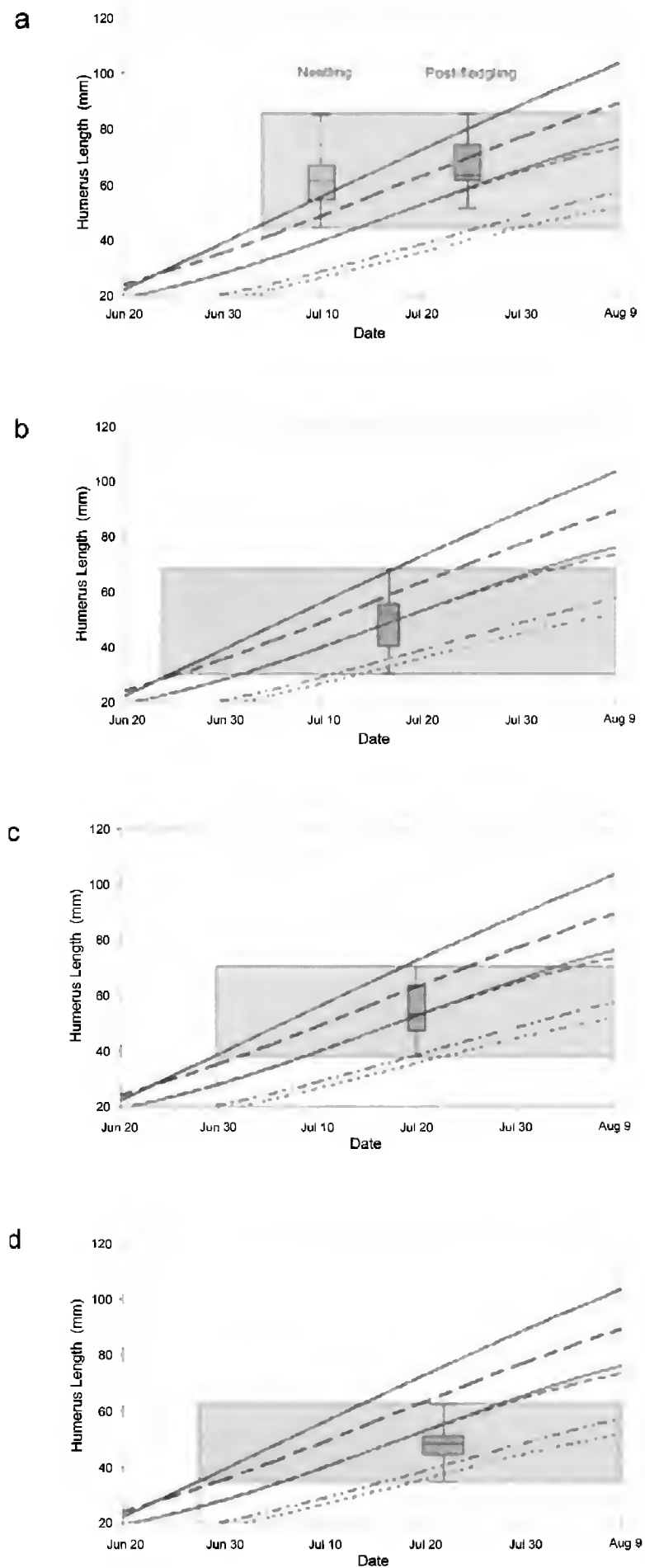


Figure 3. The size range of humeri of grouse chicks in the diet of raptors in relation to fledging dates of raptors: (a) goshawk, (b) sparrowhawk, (c) buzzard, and (d) harrier. The boxes contain the median and the 50% of values falling between 25th and 75th percentiles, the whiskers represent the highest and the lowest value. The position of the boxes on the date scale correspond to the mean fledging date and the width of the boxes is $2 \times SE$ (same as horizontal bars in Fig. 2). The growth curves

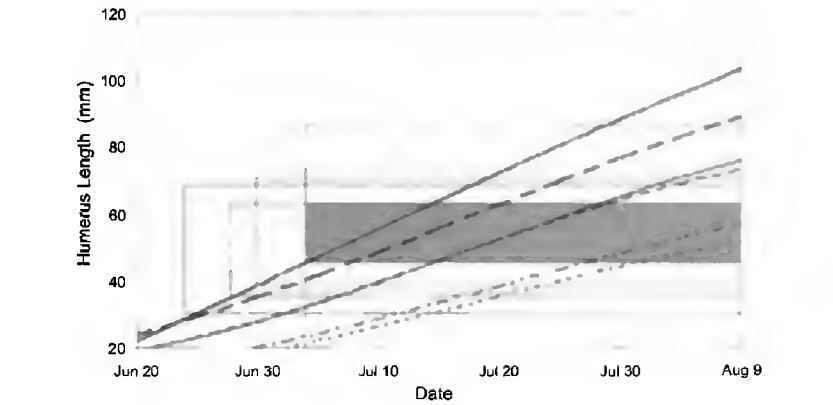


Figure 4. Overlap of size range of humeri of grouse chicks in the diet of raptors. The empty boxes are the size range (correspond to the shaded boxes in Fig. 3) and the growth curves of grouse species as in Fig. 2. The overlap (the shaded zone) indicates the time period when all the raptor species can hunt the grouse of given size range.

is suitable for the goshawk, while in August chicks of the smallest grouse species, Hazel Grouse, are also large enough to be taken (Fig. 3a). This fits with S. Sulkava's (1964) and Tornberg's (2001) findings that goshawks hunt chicks of Capercaillie and Black Grouse relatively more frequently than smaller grouse species. However, the mean size of juvenile grouse found in goshawk nests was larger than that of available Black Grouse and Capercaillie chicks. This could be due to feeding young hawks on the nest during post-fledging period or because of large age difference between the chicks (the youngest stays on the nest long after the older ones have left).

For sparrowhawks, grouse are not very important prey (P. Sulkava 1964). The mean size of chicks taken by sparrowhawks were closest to the size of Black Grouse (Fig. 2). This pattern appears reasonable, because grouse chicks are usually found at the end of the Sparrowhawk's nestling period, which may result from the females' hunting. At that time Black Grouse chicks are ca. the same mass as adult Hazel Grouse, which sparrowhawk females often kill in spring before laying (P. Sulkava 1964). This may have contributed to our finding that raptor female size appeared to be the best predictor for the size of juvenile grouse in the diet.

← of grouse species as in Fig. 2. The shaded boxes are the "predation zones" and indicate the whole size range of grouse in raptor diet (see Materials and Methods).

Table 2. The mean body mass of the avian predators (Cramp and Simmons 1980) and mean body mass of young grouse in raptor diet (estimated with regression model) during the raptor fledging period.

	MEAN MASS OF RAPTORS, G		MEAN MASS OF GROUSE, G	
	MALE	FEMALE	MEAN	SD
Eurasian Sparrowhawk	140	260	261	125
Northern Harrier	350	530	274	95
Common Buzzard	690	860	322	141
Northern Goshawk	860	1410	428	146

Grouse, especially juveniles, are important alternative prey for the Common Buzzard (Reif et al. 2001), which took on average larger grouse chicks than sparrowhawks (Fig. 2). The buzzard is capable of hunting even adult Black Grouse (Reif et al. 2001). Therefore, at the end of nestling period the maximal size of grouse in the buzzard’s diet most likely was limited by available chicks in the field (Fig. 3c). Thus, during the post-fledging period, buzzards probably hunt larger grouse chicks too. Scanty data for harriers also suggested that grouse were a fairly prominent part in their diet during poor vole years (Thirgood et al. 2000, R. Tornberg and K. Huhtala unpubl. data). The mean sizes of chicks found in the harrier’s diet corresponded best to those of Black Grouse chicks (Fig. 3d). However, they could be also large chicks of Willow Grouse, because the habitat used by both species was similar (Redpath and Thirgood 1999).

Based on the size ranges of grouse in the diet of these four raptors, in the course of development, grouse chicks undergo predation pressure by all raptor species studied. The smallest chicks are preyed upon by sparrowhawks only (Fig. 3b). Later on, while growing, they reach the size suitable for harriers and buzzards (Figs. 3c, 3d). Finally, juvenile grouse suffer from the heaviest predation (by all four raptors) when they reach the size hunted by goshawks (Fig. 3a) and thus fall within the “four-species predation zone” (Fig. 4). Chicks of different grouse species become vulnerable to goshawk predation at different ages (i.e., the youngest were Capercaillie and the oldest were Hazel Grouse). The time periods when chicks were under predation pressure by all four raptor species also varied according to the growth patterns in grouse (Fig. 4). While juvenile Capercaillie escape

from harrier predation in 10–15 d, chicks of Willow Grouse stay in the “four-species predation zone” more than 30 d and all Hazel Grouse chicks older than 40 d and adults can be preyed upon by all the raptors. Thus, predation pressure on juvenile grouse from the assemblage of the avian predators would not be even; smaller grouse species are under heaviest predation during a longer period than larger grouse. However, the correspondence of the mean size of grouse chicks in the diet of raptors at the end of their nestling periods to available juvenile grouse in the wild suggests that juvenile Black Grouse are preyed upon by most of these raptor species—sparrowhawks, buzzards, and harriers (Fig. 2). Although the goshawk certainly takes the largest share of grouse, the other three predators may have a high cumulative effect, especially in years of poor vole abundance when buzzards and harriers switch to juvenile grouse as their alternative prey.

We acknowledge that there were possible biases in our data. Because of the scarcity of grouse remains, we had to use each grouse chick found in the nest as a unit for the analysis. Multiple grouse remains in one nest cannot be considered independent, because more than likely they were taken by the same hawk. Furthermore, in some samples the sizes of grouse bones were very close to each other, which may be due to the fact that the prey belonged to the same brood (i.e., once found, the whole brood may have been killed by the same raptor). However, because the numbers of grouse chicks found per nest were low (Table 1), we believe that these limitations have not resulted in serious pseudoreplication. Moreover, we suggest that the small sample sizes of the data we used most likely affected the evaluation of hunting capabilities of raptors only as an underestimation of maximum and minimum sizes of grouse. Because the upper limit of the “four-raptor predation zone” is defined by the size of juvenile grouse in the harrier’s diet, underestimation of maximum grouse sizes in other raptors would not have an affect on determining the heaviest predation period.

In conclusion, we have found that several birds of prey share by size a common resource, grouse chicks, during their nestling periods. Juvenile grouse were vulnerable to different avian predators in the course of their development. Our data clearly indicate that the impact of predation of the whole raptor community on grouse needs to be considered when examining predation on grouse.

ACKNOWLEDGMENTS

We are grateful to Erkki Korpimäki for the idea of this study and to Sven Jungell for providing the prey and ringing material. Markku Hukkanen and the Ringing Centre of the Natural Museum of Helsinki University provided the ringing data. Pekka Helle communicated information on the hatching dates of grouse and Arto Marjakangas provided his unpublished data. Mikko Mönkkönen, Harto Lindén, and two anonymous referees gave valuable comments on the early versions of the manuscript. The study at various stages was financially supported by the Centre for International Mobility (CIMO) of the Finnish Ministry of Education, the Jenny and Antti Wihuri Foundation, and the Environmental Graduate School of EnviroNet of the University of Oulu (to V. Reif).

LITERATURE CITED

- ANGELSTAM, P., E. LINDSTRÖM, AND P. WIDÉN. 1984. Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia* 62:199–208.
- CRAMP, S. AND K.E.L. SIMMONS (EDS.). 1980. The birds of the western Palearctic. Vol. 2. Oxford Univ. Press, Oxford, U.K.
- DEMENT'EV, G.P. AND N.A. GLADKOV (EDS.). 1951. Birds of the Soviet Union. Vol. 1. Israel Program for Scientific Translations, Jerusalem, Israel.
- GRØNNESBY, S. AND T. NYGÅRD. 2000. Using time-lapse video monitoring to study prey selection by breeding goshawks *Accipiter gentilis* in central Norway. *Ornis Fenn.* 77:117–129.
- HÖGLUND, N. 1964. Über die Ernährung des Habichts (*Accipiter gentilis* L.) in Schweden. *Viltrevy* 2:271–328.
- HUHTALA, K., E. PULLIAINEN, P. JUSSILA, AND P.S. TUNKKARI. 1996. Food niche of the Gyr Falcon *Falco rusticolus* nesting in the far north of Finland as compared with other choices of the species. *Ornis Fenn.* 73:78–87.
- KENWARD, R.E., V. MARCSTRÖM, AND M. KARLBOM. 1993. Post-nestling behaviour in goshawks *Accipiter gentilis*: the causes of dispersal. *Anim. Behav.* 46:365–370.
- , R.H. PFEFFER, M.A. AL-BOWARD, N.C. FOX, K.E. RIDDLE, E.A. BRAGIN, A. LEVIN, S.S. WALLS, AND K.H. HODDER. 2000. Setting harness sizes and other marking techniques for falcon with strong sexual dimorphism. *J. Field Ornithol.* 72:244–257.
- KLAUS, S., H.-H. BERGMANN, C. MARTI, F. MÜLLER, O.A. VITOVIC, AND J. WIESNER. 1990. Die Birkhühner. Wittenberg Lutherstadt, Ziemsen, Germany.
- KORPIMÄKI, E., K. HUHTALA, AND S. SULKAVA. 1990. Does the year-to-year variation in the diet of Eagle and Ural Owls support the alternative prey hypothesis? *Oikos* 58:47–54.
- LINDÉN, H. 1981. Growth rates and early energy requirements of captive juvenile Capercaillie, *Tetrao urogallus*. *Finn. Game Res.* 39:53–67.
- . 1983. Metson ja teeren muna- ja pesyekoon vaihtelusta. (Variations in clutch size and egg size of Capercaillie and Black Grouse.) *Suomen Riista* 30:44–50.
- MARJAKANGAS, A. AND L. TÖRMÄLÄ. 1997. Female age and breeding performance in a cyclic population of Black Grouse *Tetrao tetrix*. *Wildl. Biol.* 3:195–203.
- MOSS, D. 1979. Growth of nestling Sparrowhawks (*Accipiter nisus*). *J. Zool. Lond.* 187:297–314.
- NIELSEN, O.K. 1999. Gyrfalcon predation on Ptarmigan: numerical and functional responses. *J. Anim. Ecol.* 68:1034–1050.
- REDPATH, S.M. AND S.J. THIRGOOD. 1999. Numerical and functional responses in generalist predators: Hen Harriers and peregrines on Scottish grouse moors. *J. Anim. Ecol.* 68:879–892.
- REIF, V., R. TORNBERG, S. JUNGELL, AND E. KORPIMÄKI. 2001. Diet variation of Common Buzzards in Finland supports the alternative prey hypothesis. *Ecography* 24:267–274.
- SEMENOV-TIAN-SHANSKY, O.I. 1959. On ecology of tetraonids. Lapland State Reserve, Moscow, U.S.S.R.
- SULKAVA, P. 1964. Varpushaukan pesimisaikaisesta käyttäytymisestä ja ravinnosta. *Suomen Riista* 17:93–105.
- SULKAVA, S. 1964. Zur nahrungsbiologie des habichts, *Accipiter gentilis*. *Aquilo Ser. Zool.* 3:1–103.
- , K. HUHTALA, P. RAJALA, AND R. TORNBERG. 1998. Changes in the diet of the Golden Eagle *Aquila chrysaetos* and small game populations in Finland in 1957–96. *Ornis Fenn.* 76:1–16.
- THIRGOOD, S.J., S.M. REDPATH, P. ROTHERY, AND N.J. AEBISCHER. 2000. Raptor predation and population limitation in red grouse. *J. Anim. Ecol.* 69:504–516.
- TORNBERG, R. 1997. Prey selection of the Goshawk *Accipiter gentilis* during the breeding season: the role of prey profitability and vulnerability. *Ornis Fenn.* 74:15–28.
- . 2001. Pattern of goshawk *Accipiter gentilis* predation on four forest grouse species in northern Finland. *Wildl. Biol.* 7:245–256.
- VON HAARTMAN, L., O. HILDÉN, P. LINKOLA, P. SOUMALAINEN, AND R. TENOVUO. 1963–72. Pohjolan linnut varikuvien. Vol. 4–5. Otava, Helsinki, Finland.

Received 2 December 2002; accepted 7 April 2004

Associate Editor: Juan José Negro

VARIATION IN MITOCHONDRIAL DNA OF FOUR SPECIES OF MIGRATORY RAPTORS¹

ELISE V. PEARLSTINE²

University of Florida, IFAS, 3205 College Ave., Davie, FL 33314 U.S.A.

ABSTRACT.—Four species of North American raptors, the Sharp-shinned Hawk (*Accipiter striatus*), Cooper's Hawk (*A. cooperii*), Red-tailed Hawk (*Buteo jamaicensis*), and American Kestrel (*Falco sparverius*) are migratory and utilize established flyways for summer and fall migrations. I used restriction-fragment analysis of mitochondrial DNA from individuals from each of these four species on two western and one eastern migratory flyway to test for genetic differences indicative of separation of eastern and western populations. Although the differences were small, western migratory Red-tailed Hawks possessed different mtDNA haplotypes than eastern individuals. There were no consistent differences between eastern and western individuals of the other three species. Further analyses of widespread migratory species of raptor are clearly indicated using other appropriate techniques.

KEY WORDS: *American Kestrel*; *Falco sparverius*; *Cooper's Hawk*; *Accipiter cooperii*; *Sharp-shinned Hawk*; *Accipiter striatus*; *genetic variation*; *mitochondrial DNA*; *RFLP*.

VARIACIÓN DEL ADN MITOCONDRIAL EN CUATRO ESPECIES DE RAPACES MIGRATORIAS

RESUMEN.—Cuatro especies de aves rapaces norteamericanas (*Accipiter striatus*, *A. cooperii*, *Buteo jamaicensis*, y *Falco sparverius*) son migratorias y utilizan rutas establecidas para su migración de primavera y otoño. Utilicé un análisis de ADN mitocondrial de fragmento restringido de individuos de cada una de estas cuatro especies en dos rutas de migración del oeste y una del este, para probar las diferencias genéticas indicativas de una separación entre las poblaciones de este y el oeste. Aunque las diferencias fueron pequeñas, los gavilanes colirrojos migratorios del oeste tuvieron Haplotipos del ADN mitocondrial diferentes a los del este. No hubo diferencias consistentes entre individuos del resto de especies. Un análisis mas amplio de especies migratorias de aves rapaces son claramente indicados mediante la utilización de técnicas apropiadas.

[Traducción de César Márquez]

Many North American raptor species are migratory and may fly distances of hundreds to thousands of kilometers to their wintering habitat. Some are separated into distinct geographical races or subspecies; the Red-tailed Hawk (*Buteo jamaicensis*) for example, has had a total of 14 races described for northern and central America (Preston and Beane 1993). Other raptor species are not as geographically differentiated, but one to several geographic races may be recognized. Migratory birds have been traditionally assumed to have high levels of gene flow due to their high mobility (Ar-

guedas and Parker 2000), presumably resulting in low levels of genetic diversity, and they have been relatively ignored in phylogeographic studies (Kimura et al. 2002). A few studies of migratory birds have found recognizable markers in some populations (Haig et al. 1997, Milot et al. 2000, Kimura et al. 2002) or a mixed pattern of population separation in shorebird species (Wenink et al. 1994, Haig et al. 1997). Species with northern distributions have also been shown to have shallow population structure owing to probable post-Pleistocene colonization events (Zink 1996).

Many studies have used the mitochondrial genome (mtDNA) or genomic DNA to assess population genetic structure (Wenink et al. 1994, Zink 1996, Haig et al. 1997, Arguedas and Parker 2000, Milot et al. 2000, Kimura et al. 2002). Restriction analyses of mtDNA involve the cleaving of the mitochondrial genome at sites varying from four to

¹ This research was supported by the Florida Agricultural Experiment Station, and approved for publication as Journal Series No. R-10273.

² Research conducted as Elise V. Schmidt, 4505 Maryland Parkway, Las Vegas, NV 89154 U.S.A.; current e-mail address: epearls@ufl.edu

six base pairs in length. If the sequence of base pairs is the same, cleavage fragments of identical size are created. These differences can be visualized for comparison using agarose-gel electrophoresis (Quinn 1997). Differences in sequence between individuals at these restriction sites will result in different fragment sizes. This provides a quick assessment of a percentage of the mitochondrial genome depending on how many restriction enzymes are used.

If migratory raptors are maintaining distinct populations by returning to the same breeding grounds every spring, these differences should result in separation of mtDNA lineages. Genetic differences may not exist if migratory individuals are not maintaining distinct populations, if they have a recent history of colonization in the north, or if there has been a recent bottleneck in the populations as that found in chickadees (*Poecile* spp.; Gill et al. 1993).

The Sharp-shinned Hawk (*Accipiter striatus*), Cooper's Hawk (*A. cooperii*), Red-tailed Hawk (*Buteo jamaicensis*), and American Kestrel (*Falco sparverius*) are found throughout North America with many populations exhibiting north-south migration in response to seasonal changes. Although migratory birds travel long distances and experience mixing of individuals from different areas on the wintering grounds, in some cases, such as Dunlins (*Calidris alpina*; Wenink et al. 1993, 1996, Haig et al. 1997) and Snow Geese (*Chen caerulescens*; Quinn 1992), breeding populations remain distinct. This is not true for all species; shorebirds with differing mating systems and degrees of natal philopatry exhibited varying degrees of population differentiation (Haig et al. 1997). In raptors, which generally exhibit natal philopatry (Newton 1979), North American populations may remain distinct. Here I address the question, are migratory raptors maintaining distinct populations? If so, is this pattern consistent across different taxa? And, does it reflect variation in morphology?

In this study, I examined patterns of variation of neutral molecular markers within four species of migratory raptors to determine if they are maintaining distinct differences between eastern and western populations. Migratory individuals of all four species sampled on eastern and western flyways exhibit significant morphological differences (Pearlstone in press) and the Red-tailed Hawk is polytypic with a distinctive eastern and western subspecies (Preston and Beane 1993). I sampled

individuals from two migratory routes in western North America and one on the east coast. Haplotype variation was used to provide an indication of potential population separation between raptors using different flyways.

STUDY AREA

The Goshute Mountains of Nevada and the Manzano Mountains of New Mexico are monitoring points along major raptor flyways in the west (Hoffman et al. 2002), and Cape May Point in New Jersey is situated on a major eastern flyway (Clark 1985). The Goshute and Manzano Mountain flyways are both situated along ridge systems. Migrants through Cape May Point build up along the Atlantic coastline and funnel along the southern New Jersey peninsula to cross the ocean at the point. Based on available band returns, breeding grounds are thought to be north of the western flyways (Smith et al. 1990, Hoffman et al. 2002) and north and east of the eastern flyway (Clark 1985, W. Clark pers. comm.). Goshute and Manzano migrants travel each fall to wintering grounds in central and western Mexico, a distance that may be as much as twice that of eastern migrants, which tend to remain in the southeastern United States (Clark 1985, Smith et al. 1990, and W. Clark pers. comm.).

METHODS

I took blood samples from 142 individual birds during migration in the fall of 1993–95 on each of the three flyways. These were frozen or preserved in a lysis buffer (100 mM Tris—HCL, pH 8.0, 100 mM EDTA, 10 mM NaCl, 0.5% SDS) and DNA was isolated using a standard phenol-chloroform extraction. The gene region of interest included the ND2 gene, five tRNA genes, and part of the COI gene (about 2150 base pairs). Samples were amplified by PCR using primers and PCR protocols from Riddle et al. (1993; also see Hillis and Moritz 1990). These samples were digested with 18 four-base restriction enzymes (Promega, Inc. Madison, WI U.S.A.; Table 1). Samples were electrophoresed through 1.2% agarose gel and fragments were visualized with ethidium bromide. Resultant restriction digest fragments were sized relative to a standard 1-kb ladder-molecular-weight marker. Fragment patterns were used to infer restriction sites (Dowling et al. 1990). Fragments resulting from digestion with a single restriction enzyme were assumed to result from cleavage at identical sites if the fragments were of equal size. The composite haplotype for each individual was recorded using a different letter for distinct patterns for each restriction endonuclease. I calculated genotypic divergence following the method of Upholt (1977). Haplotype diversity was calculated following the methods outlined in Ball and Avise (1992). All work was done in the laboratory of Drs. B.R. Riddle and A.P. Martin at the University of Nevada, Las Vegas, NV.

RESULTS

The ND2/COI region of the mtDNA was estimated to be ca. 2200 bp or ca. 7.5% of the 16 500 bp mitochondrial genome. I scored a total of 35 sites in all individuals giving information on about

Table 1. Haplotype composition, overall frequency, and frequency within flyways. Common haplotypes are indicated by the letter A for Sharp-shinned Hawks, Red-tailed Hawks, and American Kestrels; for the Cooper's Hawk, the common haplotype is indicated by the letter B, where it is different from that of Sharp-shinned Hawks for the same restriction enzyme.

HAPLOTYPE		HAPLOTYPE FREQUENCY			
		OVERALL	GOSHUTE MTNS.	MANZANO MTNS.	CAPE MAY POINT
Sharp-shinned Hawks ^a					
Haplotype 1	A A A A A A A A A A A A A A A A	0.82	0.73	1.00	0.75
Haplotype 2	A A A A A A A A B A A A B A A A A	0.03	—	—	0.08
Haplotype 3	A A A A A A A A A A B A A A A A	0.03	0.09	—	—
Haplotype 4	A A A A A A A A A A A B A A A A	0.12	0.18	—	0.17
Cooper's Hawks ^b					
Haplotype 1	B B A B A B A B C A A B B B B B	0.86	1.0	0.87	0.71
Haplotype 2	B C A B A B A B C A A B B B B B	0.14	—	0.13	0.29
Red-tailed Hawks ^c					
Haplotype 1	A A A A A A A A A A A A A A A	0.27	0.63	0.25	—
Haplotype 2	A B A A A A A A A A A A A A A	35	0.37	0.75	—
Haplotype 3	A B A A A A A A A A A A A A B	0.38	—	—	1.00
American Kestrels ^d					
Haplotype 1	A A A A A A A A A A A A A A A	0.97	1.0	1.0	0.91
Haplotype 2	A A A A A A A B A A A A A A A	0.03	—	—	0.09

^a Enzymes used: *AccI*, *AhaI*, *AvaII*, *BfaI*, *Bsp1286I*, *BstNI*, *BstUI*, *DdeI*, *HaeIII*, *HhaI*, *HincII*, *HinfI*, *HpaI*, *MboI*, *NlaIII*, *RsaI*, and *TaqI*.
^b Enzymes used: *AccI*, *AhaI*, *BfaI*, *Bsp1286I*, *BstNI*, *BstUI*, *DdeI*, *HaeIII*, *HhaI*, *HincII*, *HinfI*, *HpaI*, *MboI*, *NlaIII*, *RsaI*, and *TaqI*.
^c Enzymes used: *AccI*, *AhaI*, *AvaII*, *BfaI*, *Bsp1286I*, *BstNI*, *BstUI*, *DdeI*, *HaeIII*, *HhaI*, *HincII*, *HinfI*, *MboI*, *NlaIII*, and *RsaI*.
^d Enzymes used: *AccI*, *AhaI*, *AvaII*, *BfaI*, *Bsp1286I*, *BstNI*, *DdeI*, *HaeIII*, *HhaI*, *HincII*, *HinfI*, *HpaI*, *MboI*, *NlaIII*, and *TaqI*.

1.3% of the mtDNA genome, except for the American Kestrel (see below).

Sharp-shinned Hawks. I tested 34 individuals and found no apparent genetic structuring of populations. Twenty-eight individuals (82%) from all three flyways shared the same haplotype (Table 1). Of the 17 four-base restriction enzymes used, four yielded different fragment lengths in a total of six individuals. Rare haplotypes were found in one Cape May migrant and one Goshute migrant. Two individuals from Cape May Point and two from the Goshute Mountains exhibited a third unique haplotype. All haplotypes differed by only one restriction site except for one Cape May migrant that differed by two. Haplotype differences are small and haplotype diversities are low. Mean genetic distance (p) for the Sharp-shinned Hawks was 0.0003 with a haplotype divergence of 0.32 (Table 2).

Cooper's Hawks. I examined 44 individuals and found no apparent genetic structuring of populations. Thirty-six (82%) shared the same haplotype (Table 1). Of the 16 restriction enzymes used, only

one alternative haplotype that differed by a single restriction site was identified. Two Manzano migrants and four Cape May migrants exhibited this haplotype. The frequency of haplotypes was proportionately different between flyways but these differences are slight. Mean distance of haplotypes was 0.003 and divergence between haplotypes was 0.24 (Table 2).

Comparison of Sharp-shinned and Cooper's Hawks. These species differed from each other for 11 of the 15 enzymes used, ca. 17 sites (Table 1). Mean genetic distance between the two species was 0.06. Given the divergence detected between species, the low within species diversity is not due to lack of ability to detect variation for the restriction enzymes used. Relative to the scale of divergence between species, the divergence within species appears to be very recent.

Red-tailed Hawks. For 26 individuals tested there was evidence of genetic population structure between individuals using eastern and western flyways. From the 15 four-base restriction enzymes

Table 2. Summary of genetic characteristics and haplotype diversity. Genotypic diversity = $(n/[n-1]) (1-3f_i^2)$, where f_i is the frequency of the i th mtDNA haplotype (Ball and Avise 1992). $p = 1 - [0.5(-F + \{F^2 + 8F\}^{0.5})]^{1/r}$, where $F = 2N_{xy}/(N_x + N_y)$ and r is the number of base pairs in the enzyme's recognition site (Avise 1994). All enzymes used recognized four base pairs.

SPECIES	<i>N</i>	NO. HAPLOTYPES/ INDIVIDUAL	GENOTYPIC DIVERSITY	NUCLEOTIDE DIVERSITY (<i>p</i>)
Sharp-shinned Hawk	34	0.12	0.32	0.0004
Cooper's Hawk	44	0.05	0.24	0.0003
Red-tailed Hawk	26	0.12	0.69	0.0090
American Kestrel	38	0.05	0.06	0.0001

used, two (*AluI* and *RsaI*) yielded different fragment lengths. Of the haplotypes identified, one was specific for the Cape May migrants and differed from one of the western haplotypes by one restriction site (Table 1). In the western migrants, there were two mtDNA haplotypes, both of which showed variation in frequency between Goshute and Manzano migrants. Haplotype A was found in 27% of the individuals, and haplotype B in 35% of the individuals. The third haplotype constituted 38% of the samples and was found only in individuals from Cape May Point. This geographic structure, although slight, indicates a consistent separation of eastern and western migratory Red-tailed Hawks. Individuals from the two western flyways did not differ in haplotype composition, but did in frequency of haplotypes. Mean genetic distance was 0.09 and haplotype diversity was 0.686 (Table 2).

American Kestrels. I tested 38 individuals and found no apparent population genetic structure. Fifteen restriction enzymes recognized ca. 30 restriction sites. This represents a little less than 1.2% of the mtDNA genome. Birds from all flyways had a single, common haplotype (Table 1) with the exception of one individual from Cape May Point that differed from the rest by one restriction site. Genetic distance is 0.0001 and haplotype diversity is 0.06 (Table 2).

DISCUSSION

Patterns of mtDNA restriction-fragment length polymorphisms that may be indicative of phylogeographic structure were found only in the Red-tailed Hawk. In this species, the eastern individuals all differed by a single restriction site from all western individuals although haplotype diversity was low. This corresponds with distributions of subspecies

calurus and *borealis* (Preston and Beane 1993); all individuals exhibited morphological characters consistent with subspecies designations for their geographic area. Other studies have found eastern/western population differences in migratory warblers (Milot et al. 2000, Kimura et al. 2002) and European Rock Partridges (Lucchini and Randi 1998).

Although I found substantial differences between the two species of *Accipiter*, no population structure was detected within Sharp-shinned and Cooper's hawks. I found similar results for American Kestrels. There may be no actual population structure in these species or the methods used may not have been sensitive enough to detect the presence of different mtDNA haplotypes. These three species are all characterized by a number of subspecies, but only one occurs within the area covered by this study.

Genetic distances within and between species were within the range of distances found for other North American bird species with a primarily northern distribution, such as chickadees (Gill et al. 1993) and redpolls (*Carduelis* spp.; Seutin et al. 1995), and for bird species with a wide North American distribution (Ball and Avise 1992, Zink 1996). Differences were low compared with two species of migratory warblers, Yellow Warbler (*Dendroica petechia*; Milot et al. 2000), and Wilson's Warbler (*Wilsonia pusilla*; Kimura et al. 2002). As in this study, some bird species with a northern distribution do not exhibit clear phylogeographic structure (e.g., Avise et al. 1992, Gill et al. 1993, Seutin et al. 1995), whereas others do (Van Wagner and Baker 1990, Zink 1994, Lucchini and Randi 1998).

Future work on the population structure of raptors is clearly indicated. The application of newer

techniques such as microsatellites, which are appropriate for this level of study (McDonald and Potts 1997, Arguedas and Parker 2000, Baker 2000, Milot et al. 2000), should be applied. Also, further investigation of the control region may serve to confirm the results of this restriction fragment length polymorphism (RFLP) study (Wenink et al. 1994, Baker and Marshall 1997) and perhaps provide more information on geographic population structure of North American raptors. Lucchini and Randi (1998) used mtDNA control region sequencing for population level studies of Rock Partridges in Europe and found that populations have remained separate since glacial recolonization. A study of shorebirds using randomly amplified polymorphic DNA (RAPD) analysis assisted in assigning individuals of some species to breeding locations (Haig et al. 1997). Further investigation into the genetic basis of subspecies designations in Red-tailed Hawks may also provide important information on the possible genetic basis of morphological differences.

ACKNOWLEDGMENTS

I wish to thank several anonymous reviewers for helpful comments on this paper. This study could not have been completed without the assistance of Daniel B. Thompson, Charles L. Douglas, Brett R. Riddle, Donald H. Baepler, Clayton M. White, and James E. Deacon. Personnel from HawkWatch International and Cape May Point were an integral part of this study. Special thanks go to Stephen Hoffman, William C. Clark, Chris Schultz, Phil Magasich, and Paul A. Napier. Funding was provided by a doctoral dissertation improvement grant (DEB 9321656), the Stephen R. Tully Memorial Grant from the Raptor Research Foundation, Arizona-Nevada Academy of Sciences, HawkWatch International, the University of Nevada, Las Vegas (UNLV) Graduate College, the Department of Biological Sciences at UNLV, and the Marjorie Barrick Museum at UNLV. Support was also provided by the Marjorie Barrick Fellowship at UNLV and the Women in Science Award, UNLV.

LITERATURE CITED

- ARGUEDAS, N. AND P.G. PARKER. 2000. Seasonal migration and genetic population structure in House Wrens. *Condor* 102:517–528.
- AVISE, J.C. 1994. Molecular markers, natural history and evolution. Chapman and Hall, New York, NY U.S.A.
- , R.T. ALISAUSKAS, W.S. NELSON, AND C.D. ANKNEY. 1992. Matriarchal population genetic structure in an avian species with female natal philopatry. *Evol.* 46: 1084–1096.
- BAKER, A.J. 2000. Molecular ecology. Pages 1–6 in A.J. Baker [ED.], *Molecular methods in ecology*. Blackwell Science, Ltd., Oxford, U.K.
- AND H.D. MARSHALL. 1997. Mitochondrial control region sequences as tools for understanding evolution. Pages 51–82 in D.P. Mindell [ED.], *Avian molecular evolution and systematics*. Academic Press, Ltd., San Diego, CA U.S.A.
- BALL, M.R., JR. AND J.C. AVISE. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the evolutionary significance of subspecies. *Auk* 109:626–636.
- CLARK, W.S. 1985. The migrating Sharp-shinned Hawk at Cape May Point: banding and recovery results. Pages 137–148 in M. Harwood [ED.], *Proceedings of hawk migration conference IV*. Hawk Migration Association of North America, Washington Depot, CT U.S.A.
- DOWLING, T.E., C. MORITZ, AND J.D. PALMER. 1990. Nucleic acids II: restriction site analysis. Pages 250–317 in D.M. Hillis and C. Moritz [EDS.], *Molecular systematics*. Sinauer Associates, Inc., Sunderland, MA U.S.A.
- GILL, F.B., A.M. MOSTROM, AND A.L. MACK. 1993. Speciation in North American chickadees: patterns of mtDNA genetic divergence. *Evol.* 47:195–212.
- HAIG, S.M., C.L. GRATTO-TREVOR, T.D. MULLINS, AND M.A. COLWELL. 1997. Population identification of western hemisphere shorebirds throughout the annual cycle. *Mol. Ecol.* 6:413–427.
- HILLIS, D.M. AND C. MORITZ. 1990. *Molecular systematics*. Sinauer Associates, Inc., Sunderland, MA U.S.A.
- HOFFMAN, S.W., J.P. SMITH, AND T.D. MEEHAN. 2002. Breeding grounds, winter ranges, and migratory routes of raptors in the mountain west. *J. Raptor Res.* 36:97–110.
- KIMURA, M., S.M. CLEGG, I.J. LOVETTE, K.R. HOLDER, D.J. GIRMAN, B. MILA, P. WADE, AND T.B. SMITH. 2002. Phylogeographical approaches to assessing demographic connectivity between breeding and overwintering regions in a Nearctic-Neotropical warbler (*Wilsonia pusilla*). *Mol. Ecol.* 11:1605–1616.
- LUCCHINI, V. AND E. RANDI. 1998. Mitochondrial DNA sequence variation and phylogeographical structure of Rock Partridge (*Alectoris graeca*) populations. *Heredity* 81:528–536.
- MCDONALD, D.B. AND W.K. POTTS. 1997. DNA microsatellites as genetic markers at several scales. Pages 51–82 in D.P. Mindell [ED.], *Avian molecular evolution and systematics*. Academic Press, Ltd., San Diego, CA U.S.A.
- MILOT, E., H.L. GIBBS, AND K.A. HOBSON. 2000. Phylogeography and genetic structure of northern populations of the Yellow Warbler (*Dendroica petechia*). *Mol. Ecol.* 9:667–681.
- NEWTON, I. 1979. *Population ecology of raptors*. Buteo Books, Vermillion, SD U.S.A.
- PEARLSTINE, E.V. AND D.B. THOMPSON. In press. Geographic variation in morphology of four species of migratory raptors. *J. Raptor Res.* in press.
- PRESTON, C.R. AND R.D. BEANE. 1993. Red-tailed Hawk (*Buteo jamaicensis*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 52. The Academy of Nat-

- ural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.
- QUINN, T.W. 1992. The genetic legacy of mother goose phylogeographic patterns of lesser Snow Goose *Chen caerulescens caerulescens* maternal lineages. *Mol. Ecol.* 1: 105–117.
- . 1997. Molecular evolution of the mitochondrial genome. Pages 3–28 in D.P. Mindell [ED.], *Avian molecular evolution and systematics*. Academic Press, San Diego, CA U.S.A.
- RIDDLE, B.R., R.L. HONEYCUTT, AND P.L. LEE. 1993. Mitochondrial DNA phylogeography in northern grasshopper mice (*Onychomys leucogaster*)—the influence of quaternary climatic oscillations on the population dispersion and divergence. *Mol. Ecol.* 2:183–193.
- SEUTIN, G., L.M. RATCLIFFE, AND P.T. BOAG. 1995. Mitochondrial DNA homogeneity in the phenotypically diverse redpoll finch complex (Aves: Carduelinae: *Carduelis flammea-hornemanni*). *Evolution* 49:962–973.
- SMITH, J.P., S.W. HOFFMAN, AND J.A. GESSAMAN. 1990. Regional size differences among fall-migrant accipiters in North America. *J. Field Ornith.* 61:192–200.
- UPHOLT, W.B. 1977. Estimation of DNA sequence divergence from comparison of restriction endonuclease digests. *Nucleic Acids Res.* 4:1257–1265.
- VAN WAGNER, C.E. AND A.J. BAKER. 1990. Association between mitochondrial DNA and morphological evolution in Canada Geese. *J. Mol. Evol.* 31:373–387.
- WENINK, P.W., A.J. BAKER, AND M.G.J. TILANUS. 1993. Hypervariable-control-region sequences reveal global population structuring in a long-distance migrant shorebird, the Dunlin (*Calidris alpina*). *Proc. Natl Acad. Sci.* 90:94–98.
- , A.J. BAKER, AND M.G.J. TILANUS. 1994. Mitochondrial control-region sequences in two shorebird species, the turnstone and the Dunlin and their utility in population genetic studies. *Mol. Biol. Evol.* 11:22–31.
- , ———, H.-U. ROSNER, AND M.G.J. TILANUS. 1996. Global mitochondrial DNA phylogeography of holarctic breeding Dunlins (*Calidris alpina*). *Evolution* 50: 318–330.
- ZINK, R.M. 1994. The geography of mitochondrial DNA variation, population structure, hybridization, and species limits in the Fox Sparrow (*Passerella iliaca*). *Evolution* 48:96–111.
- . 1996. Comparative phylogeography in North American birds. *Evolution* 50:308–317.

Received 12 September 2003; accepted 28 May 2004
Associate Editor: Juan José Negro

NESTING BIOLOGY AND DIET OF THE MADAGASCAR HARRIER (*CIRCUS MACROSCELES*) IN AMBOHITANTELY SPECIAL RESERVE, MADAGASCAR

LILY-ARISON RENE DE ROLAND, JEANNENEY RABEARIVONY, AND IGNACE RANDRIAMANGA
The Peregrine Fund's Madagascar Project, B.P. 4113, Antananarivo (101), Madagascar

RUSSELL THORSTROM¹
The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709 U.S.A.

ABSTRACT.—We studied Madagascar Harriers (*Circus macroscyles*) in the central high plateau at Ambohitantely Special Reserve, Madagascar during the 1997 and 1998 breeding seasons. We located 11 nests and documented eight nesting attempts during the two seasons. All nests were placed on vegetation within marshes ($N = 9$) and averaged 43 cm above water level. Breeding commenced in late August and September, during the middle of the dry season. Egg laying occurred from the middle of September to the end of October, peaking in late September and spanning 40 d for eight clutches. The incubation period was 32–34 d at eight nests and nestlings fledged at 42–45 d of age ($N = 7$) in November and December, at the start of the rainy season. Of 23 eggs laid in eight nests (\bar{x} clutch size = 2.9), 17 of 23 (74%) hatched, and seven (41%) of those hatchlings fledged. Overall productivity was 0.9 young fledged per breeding attempt and nest success was 75% ($N = 8$). Only one of six successful nesting attempts fledged two young. The Madagascar Harrier diet from 272 identified prey was composed of insects (48%), snakes (21%), birds (21%), lizards (6%), rodents (3%), and domestic chickens (1%); in terms of biomass based on prey remains and pellets: birds (45%), reptiles (35%), and mammals (18%) made 98% of prey. This is the first breeding study of this species, and it shows this harrier reproduces at a relatively low rate, and has an unusual diet relative to related species.

KEY WORDS: *Madagascar Harrier; Circus macroscyles; Madagascar; nests; diet; nesting behavior.*

DIETA Y BIOLOGIA DE ANIDACION DE *CIRCUS MACROSCELES* EN LA RESERVA ESPECIAL DE AMBOHITANTELY, MADAGASCAR

RESUMEN.—Estudiamos los aguiluchos de el Madagascar (*Circus macroscyles*) en la Reserva Especial de Ambohitantely, Madagascar durante las estaciones reproductivas de 1997 y 1998. Localizamos 11 nidos y documentamos ocho intentos de anidacion durante las dos estaciones. Todos los nidos fueron ubicados en vegetación de pantano ($N = 9$) y promediaron 43 CMS sobre el nivel del agua. La reproducción comenzó a finales de Agosto y Septiembre, a mediados de la estación seca. La postura de huevos ocurrió desde mediados de Septiembre hasta finales de Octubre, con un pico hasta finales de Septiembre y expandiéndose por 40 días y eight nidadas. El periodo de incubación fue de 32–34 días en ocho nidos y los pichones emplumaron a los 42–45 días de edad ($N = 7$) en Noviembre y Diciembre, al inicio de la estación lluviosa. De los 23 huevos puestos en eight nidos (tamaño de la nidada = 2.9) 17 de 23 (74%) eclosionaron y seven (41%) de los pichones emplumaron. La productividad general fue de 0.9 pichones emplumados por intento reproductivo y el éxito de anidacion fue de 75% ($N = 8$). En solo uno de seis intentos exitosos de anidacion emplumaron dos pichones. La dieta del aguilucho de Madagascar (de 272 items de presas identificadas) estuvo compuesta por insectos (48%), Serpientes (21%), aves (21%), lagartijas (6%), roedores (3%) y gallinas domesticas (1%). En términos de biomasa, con base en restos de presas y egagropilas las aves constituyeron un 45%, los reptiles un 35% y los mamíferos un 18% para un total de un 98% de presas. Este es el primer estudio sobre la reproducción de esta especie y muestra que el aguilucho se reproduce a una tasa lenta y tiene una dieta inusual comparada con las de las especies relacionadas.

[Traducción de César Márquez]

¹ Corresponding author's e-mail address: rthorstrom@peregrinefund.org

Our knowledge of the ecology and biology of Malagasy raptors has gradually increased based mostly on research in northeastern Madagascar (Thorstrom and Rene de Roland 2000); however, the biology of the Madagascar Harrier (*Circus macroscelus*) is still poorly known. The cosmopolitan group, the harriers (*Circus*), is relatively well-known 16 species of medium-sized hawks, and includes one species in Madagascar. This harrier (*C. macroscelus*) was recently separated and elevated to a full species rank by M. Wink in Simmons (2000), based on DNA evidence and morphological differences from its sister species, the Réunion Harrier (*C. maillardi*; Bretagnolle et al. 2000). The Madagascar Harrier is a rather uncommon bird of the open marshes and grasslands, and is observed infrequently coursing over grass fields, fallow rice fields, marshes, and wetlands (Langrand 1990, del Hoyo et al. 1994). Globally, it is classified as a vulnerable species (BirdLife International 2000). Its diet consists predominantly of birds, reptiles, mammals, and insects (Rand 1936, Langrand 1990). Threats to this species include dry season grassland fires that usually occur during its nesting season, loss of marsh and grassland habitat, and human persecution to protect poultry and for food (Paverne 1997, BirdLife International 2000). The population status and distribution is not well known. Here, we provide new information on the breeding biology of the Madagascar Harrier from the high central plateau region of north-central Madagascar.

STUDY AREA

We studied the Madagascar Harrier in Ambohitantely Special Reserve (18°13'S, 47°16'E) and its surrounding area during two consecutive breeding seasons, 1997–98 (Randriamanga 2000). This reserve is situated in the high central plateau, about 130 km northwest of Antananarivo, the capital of Madagascar. In 1982, the area was classified as a Special Reserve of 5600 ha (Nicoll and Langrand 1989). Of the 5600 ha, only 2800 ha are still covered by native forests, 1960 ha by grasslands including marshes, and 840 ha of exotic plantations (Langrand 1995). The eastern-facing slopes contain the native forest fragments. In the higher elevations and the western section of the reserve, the area is covered by grasslands composed of *Aristida rufescens*, *Loudetia* sp., and *Andropogon* sp., and low-lying areas of marshes with other grasses and reeds (e.g., Cyperaceae). On the knolls and summits in the western section, small stands of introduced trees of *Pinus patula* and *Eucalyptus* sp. are common. The elevation varies from 1267–1660 m. The climate is characterized by two distinct seasons; a dry warm period from April–October and a hot rainy season from November–March. The mean annual rainfall is 2150 mm and sea-

sonal temperatures range from 10–25°C (Nicoll and Langrand 1989).

METHODS

We searched marshes, valleys, and rolling hills over the whole reserve daily from July–December 1997 and August 1998–January 1999 for potential breeding pairs. We watched for harriers flying near marshes to detect pair activities and courtship behavior. We followed harriers daily by sight until a nest was confirmed by a pair's behavior or by locating the nest. Nest observations were made from the ground with 10× binoculars and 20–45× spotting scope at distances of 200 m. We observed nest sites from 0500–1830 H and rotated among nests. When accessible, we measured nest length, width, and height above water level to the nearest 1.0 cm. We considered the incubation period to be the time (d) from the laying of the penultimate egg (usually the second or third laid egg) to the hatching of the second egg (Simmons 2000). We measured length and breadth of eggs to the nearest 0.1 mm with vernier calipers and fresh egg mass to the nearest gram with a 100 g Pesola spring scale (Pesola, Jackson, MS U.S.A.). Reproductive variables and productivity were defined as: breeding attempt (nests that contained at least one egg), laying date (when the first egg was laid), clutch size per individual nest (number of eggs laid in nests), mean clutch size (mean number of eggs laid per breeding attempt), number of eggs hatched, young fledged (number of young surviving to first flight), productivity (number of young fledged per breeding attempt), and nest success (number of total breeding attempts that fledged at least one young).

Prey delivered by adults was identified and quantified during daily nest observations. Prey remains were collected from nests and were identified by S. Goodman of World Wide Fund for Nature (WWF) in Madagascar. Madagascar Harriers were trapped with a bal-chatri placed near the pair's center of activity during the breeding period (Thorstrom 1996). We determined body mass with a 1000 g Pesola spring scale and measured wing and tail length to the nearest 0.1 mm with vernier calipers or to the nearest 1 mm with a metric tape measure. Three birds were color banded for individual identification.

RESULTS

Courtship activities began in August and September. Initiation of the breeding season began with courtship flights and pairs defending a space around a site, where they intended to place a nest. We located seven nest sites in 1997 and four in 1998, of which two were on the same territories as 1997, (total of nine sites in an area ca. 1500 ha; Fig. 1). The distance between neighboring nests averaged 1514.5 m \pm 674.6 m (range = 370–3720 m, N = 9 pairs).

Courtship Behavior. Courtship behaviors consisted of intraspecific vocalizations, aerial display flights by males, pair-formation flights, nest building activities, courtship feedings, copulations, and

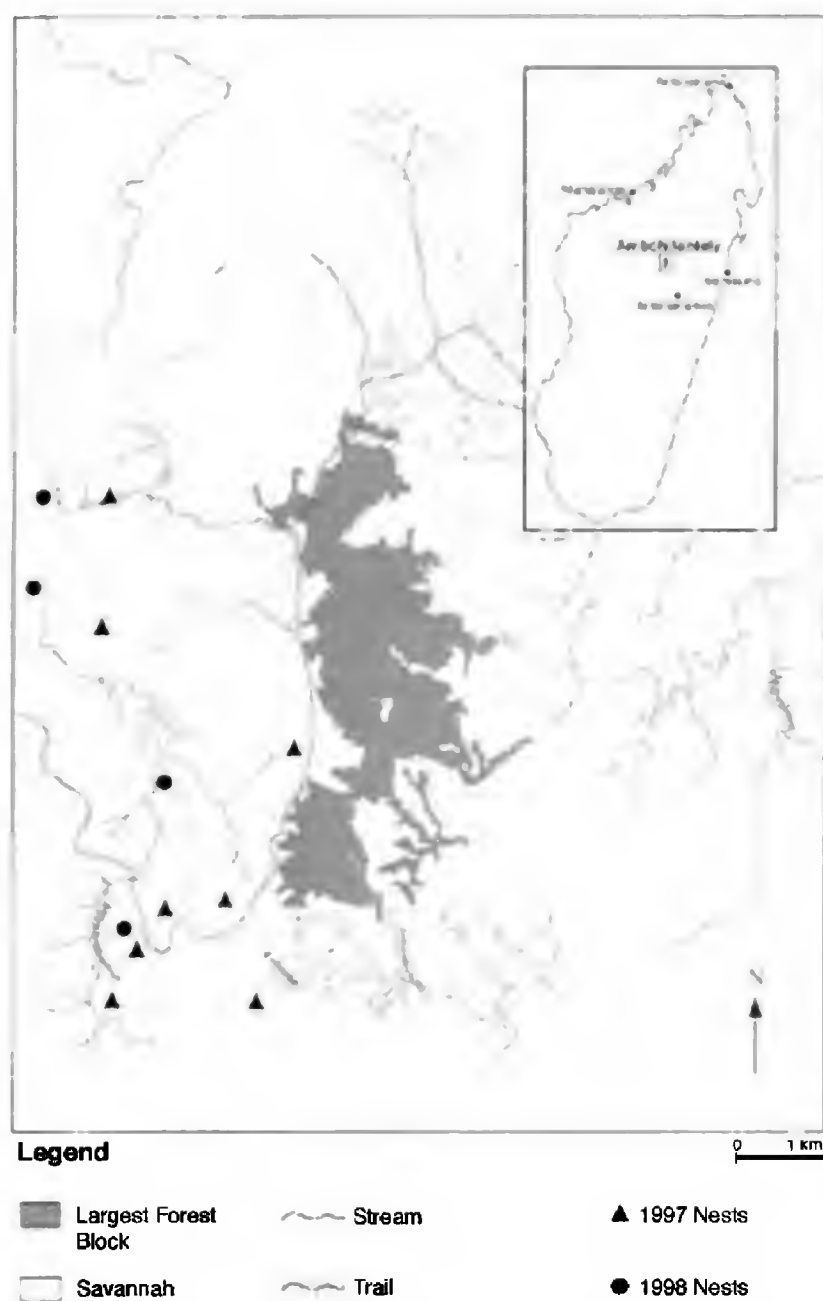


Figure 1. Location of study site, Ambohitantely Special Reserve, in Madagascar and nest locations during 1997 and 1998 breeding seasons.

nest defense. Aerial display flights began with a spiraling, ascending flight by the male, then progressed to a fast hard flapping flight with steep undulations and then to rapid descending spirals with “koue” vocalizations. The earliest pair-formation flight observed was on 12 August 1997. Pair-formation flights involved the male and female flying slowly together in their territory and sometimes stalling and grabbing at the other member of the pair. Males called “koue . . . koue” every 10–15 sec during pair-formation flights. During the courtship period the female was provisioned with food by the male. Copulations always came after a prey delivery from male to female. Copulations averaged 8.9 ± 0.9 (SE) sec in duration ($N = 12$, range = 6–15 sec) and occurred 3–4 times a day.

The territorial defense call may be described as “ouek” given ca. 5 sec when another harrier was

close to the nesting area. Also, “kêkêkêkêkê” was the sign of alarm or emitted when a predatory animal was close to the nest.

Three adults were trapped during this period. Measurements taken were: wing chord = 459 mm, 461 mm, and 443 mm; and tail = 288 mm, 285 mm, and 272 mm, for two females and one male, respectively. Madagascar Harriers show moderate reverse size dimorphism. The mass of two females were 850 and 910 g and the one male was 600 g.

Nest Building. Nest construction began 15–17 d after pair formation. The earliest nest building was observed on 26 August 1997. The male was predominantly responsible for building (quantitative data not available) the nest, while the female remained in the nest vicinity vocalizing for food. All nests were built on vegetation in marshes. Herbaceous vegetation and grasses used in nest building were collected from the ground (e.g., *Eulalia villosa*, *Osmunda regalis*, *Scirpus* spp., *Kotschyia africana*, *Aristida rufescens*, and *Pteridium* spp.), while dry twigs were collected from *Eucalyptus* and *Pinus* trees. All nesting material was collected from 40–200 m of the nest site.

Nest building activities started early morning, from 0530–0900 H, and continued again from 1700 H–sunset. Due to the level of water below nests, only nine of 11 located nests were accessible for measurements. Nest measurements averaged 63.2 ± 7.2 cm (range = 50.0–77.0 cm) by 44.5 ± 4.5 cm (range = 34.2–51.3 cm). For nine nests, the mean height above water was 43.2 ± 15.5 cm (range = 24.5–81.0 cm). Pairs built new nests every year and the mean distance between the previous year’s nest in a given territory was $575 \text{ m} \pm 205.1 \text{ m}$ ($N = 2$). Nest building took 25–30 d ($N = 11$ nests). A renesting attempt occurred at one nest 200 m from the first nest which was destroyed during the early incubation period.

Egg Laying. During the two breeding seasons, the earliest recorded laying date was 13 September 1997 with incubation starting on 15 September 1997 and the latest laying date was 20 October 1997 with incubation starting on 26 October 1997 ($N = 8$ nests). The modal clutch size was three ($N = 5$), followed by clutches of two ($N = 2$), and there was one four-egg clutch; the mean clutch size was 2.9 ± 0.2 . Mean dimensions of 23 Madagascar Harrier eggs were 48.7 ± 1.7 mm (44.1–51.0 mm) by 37.5 ± 1.1 mm (35.7–40.0 mm). Mean fresh egg mass was 36.5 ± 1.2 g (34.8–39.0 g).

Incubation. Only females incubated. In 216.3 hr

Table 1. Reproductive success of Madagascar Harriers (*Circus macroscleus*) at Ambohitantely Special Reserve, Madagascar, during the breeding seasons of 1997 and 1998.

YEAR	NESTS	BREEDING ATTEMPTS OBSERVED	NUMBER OF EGGS	MEAN CLUTCH SIZE	NO. EGGS HATCHED (%)	NO. YOUNG FLEDGED (%)	FLEDGLINGS/ BREEDING ATTEMPT	NEST SUCCESS (%) (N)
1997	7	4	12	3	10 (83%)	4 (40%)	1.00 (4/4)	100 (4)
1998	4	4	11	2.7	4 (37%)	3 (75%)	0.75 (3/4)	50 (2)
Total	11	8	23	2.9	14 (61%)	7 (50%)	0.88 (7/8)	75 (6)

of nest observations, females incubated for 196.8 hr (91%) and the nest was unattended for 19.5 hr (9%). The incubation period ranged from 32–34 d ($N = 8$ nests). During the incubation period, the male's primary role was food provisioning to the female and nest defense.

Nestling Period. At hatching, nestling mass varied from 25–32 g ($N = 6$). Brooding and feeding the young was the female's responsibility. When the male arrived with prey, he circled above the nest, and called "tou . . . tou . . . touff" to the female. Also, the female solicited food by calling "kiou . . . kiou . . . kio" Prey were delivered directly to females mostly by an aerial transfer (88.8%; $N = 166$). In several instances, when the female did not respond to the male and leave the nest or was absent, the male delivered the prey directly into the nest (11.2%). The earliest the female was observed leaving the nest and hunting for the nestlings was when the nestlings were 24 d of age. Young first flew from 42–45 d of age ($N = 7$). First flights of young were about 1–5 m from the nest.

Post-fledging Period and Dispersal. By 48 d of age, young were flying 20 m from the nest. Fledglings were always fed at the nest by the adults during the first week. At 50 d of age, the male tried transferring food to the young in flight while the female placed prey on tufts of grass averaging 136.7 ± 101.7 m ($N = 6$, range = 40–300 m) from the nest. After 50 d of age, young were not observed being fed by the females and solicited food with the "kiou" call. At 55 d of age, young flew up to a height of 100–200 m and did not return to their nests for periods of ca. 15 min. Fledglings began taking prey in flight from the male at 55 d of age. The adult females had disappeared from their nesting territories when young were ca. 65 d of age ($N = 7$ nests). Young dispersed from their natal areas at 70 d of age along with the adult male.

Reproductive Success. In eight fully-monitored

nests containing 23 eggs, 14 (61%) hatched, and seven (50%) of those hatched fledged (Table 1). In total, seven young fledged from eight breeding attempts, for an overall productivity of 0.9 young fledged. Nest success for the 2 yr of the study was 75% ($N = 8$). In 1998, two nests were destroyed by a grassland fire during incubation. Reproductive losses resulted from brood reduction (59%), addled eggs (26%), and Pied Crows (*Corvus albus*; 15%) among the eight nesting attempts. For each nest containing three young, the third individual was always dead at less than 10 d of age. In nearly all nesting attempts with two or more young, the second nestling hatched did not survive more than 40 d, and was often dead between 14–35 d of age. Only one of eight nesting attempts was successful in fledging two young.

Food Habits. We observed 272 prey items being delivered to females and nestlings during the two study seasons. On a numerical basis, insects were the predominant prey comprising 48.2% ($N = 131$) of the diet, followed by snakes 20.9% ($N = 57$), birds 20.6% ($N = 56$), chameleons (*Furcifer* spp.) 5.9% ($N = 16$), rodents 3.3% ($N = 9$), and chickens (*Gallus gallus*) 1.1% ($N = 3$). Prey remains ($N = 12$) and pellets ($N = 22$) left in the nests were identified and composed of 24% insects, 44% birds, 14% snakes, 6% chameleons, and 12% rodents and insectivores ($N = 50$ identified prey; Table 2). On a biomass basis, birds (44.7%), reptiles (35.6%), and mammals (18.6%) comprised 98.9% of the estimated biomass from prey remains and pellets (Table 2).

DISCUSSION

In this first ecological study of the breeding and diet of the Madagascar Harrier we found: nesting was limited to marshy areas of savannah habitat in Ambohitantely Special Reserve, breeding commenced in the spring (August–September) similar to other southern harriers, copulations were always

Table 2. List of prey species identified from remains and pellets of Madagascar Harriers (*Circus macrosceles*) at Ambohitantely Special Reserve, Madagascar during 1997–98.

PREY SPECIES	NO. ITEMS	BIOMASS (G)	BIOMASS TOTAL (%) AND SOURCE
INSECTS		60	1.1
Orthopteran (<i>Nomadacris septemfasciata</i>)	12	5	Estimate ^a
REPTILES		1850	35.6
Chameleon (<i>Furcifer lateralis</i>)	3	150	Estimate ^a
Snake (<i>Liopholidophis lateralis</i>)	7	200	Estimate ^a
AVES		2325	44.7
Madagascar Flufftail (<i>Sarothrura insularis</i>)	1	300	Dunning 1993
Common Quail (<i>Coturnix Coturnix</i>)	2	100	Dunning 1993
Madagascar Partridge (<i>Margaroperdix madagascarensis</i>)	4	220	Dunning 1993
Madagascar Button-quail (<i>Turnix nigricollis</i>)	1	40	Estimate ^a
Common Stonechat (<i>Saxicola torquata</i>)	2	15	Dunning 1993
Madagascar Lark (<i>Mirafra hova</i>)	3	45	Estimate ^a
Madagascar Cisticola (<i>Cisticola cherinus</i>)	1	10	Dunning 1993
Domestic chicken (<i>Gallus gallus</i>)	3	300	Estimate ^a
Unidentified birds	5		
MAMMALS		965	18.6
Black Rat (<i>Rattus rattus</i>)	4	200	Garbutt 1999
House Mouse (<i>Mus musculus</i>)	1	15	Garbutt 1999
Lowland-streaked Tenrec (<i>Hemicentetes semmispinosus</i>)	1	150	Garbutt 1999
TOTAL	50	5200	

^a Based on mass measurements taken in the field.

accompanied by prey delivery by males, clutch was typically small (2.9 eggs) for a tropical harrier, and substantial brood reduction occurred. We suggest that the relatively unusual diet for harriers comprised mainly of insects may have stimulated sibling aggression among nestlings.

In Ambohitantely Special Reserve, the topography of the area has led to irregular formation of marshes and valleys, thus restricting the nesting area for Madagascar Harriers. On the other hand, the aggressiveness of males toward conspecifics also seemed to result in the spacing of nesting pairs. Grasses, herbaceous vegetation and dry branches, from *Pinus* and *Eucalyptus* spp. trees, were utilized for nest construction by the harriers, same as reported by Paverne (1997) in Madagascar. Madagascar Harriers placed nests on grass tufts in marshes, which facilitated nest construction, similar to other marsh harrier species (Simmons 2000). The Madagascar Harrier nests were about 40 cm above the water level.

In Réunion, a small island 700 km east of Madagascar, the Réunion Harrier, a sister species to the Madagascar Harrier, began the breeding season at the same time as the Madagascar Harrier with courtship displays in August–September, nest building in October–November and onward, egg laying from January–April, and fledglings reported with adults up to October (Bretagnolle et al. 2000). Compared to the Madagascar Harrier, the Réunion Harrier had a prolonged breeding season. Harriers in Madagascar at Ambohitantely Special Reserve, commenced breeding with courtship beginning in August–September, and nest construction and egg laying in September–October, at a time when the water level in marshes was at its minimum. Paverne (1997) also had two nests underway in September and one in November 1996, in the same general region as Ambohitantely. Paverne (1997) reported on two nests with four and two eggs each, and one with undetermined number of eggs or young. We suspect the nest located in November (Paverne

1997) might possibly have been a renesting attempt due to the timing of the incubation period we recorded and the second nesting attempt we documented. By the time the rainy season began in late November and December, and water level in the marshes began rising, young harriers had fledged (first flights) or were near fledging. For the Réunion Harrier, fledging appeared to occur from March–June, and much later than our observations for Madagascar Harriers.

For Madagascar Harriers, hatching success averaged 61% for both years, and was extremely low (37%) during the 1998 breeding season due to grassland fires destroying several nests and the presence of addled eggs. The female fed and cared for the first-hatched nestling immediately, and we believe this led to a decrease of incubation time of the remaining eggs, possibly causing the high incidence of addled eggs (39%).

Simmons (2000) showed that all harrier species exhibit reverse size dimorphism, and we found Madagascar Harrier females have one of the largest body sizes, at 850–910 g, of the 16 harrier species found in the world.

Probably due to limited food and aggressive behavior from the first-hatched nestling, the second and third hatched young died at 35 and 10 d of age ($N = 2$ nests), respectively. The weakest young were killed by the first-hatched nestlings, similar to many other raptors living in food restricted environments (Meyburg 1974, Simmons 1988, Gargett 1990). Brood reduction is well documented for other harrier species as well (Simmons 2000).

Previous reports on the food habits of the Madagascar Harrier came from four stomach contents examined by Rand (1936), who found the head and feet of a Madagascar Partridge (*Margaroperdix madagascarensis*), a rat (*Rattus* sp.), fur of a small mammal, two frogs, a young whistling duck (*Dendrocygna* sp.), and an insectivorous mammal.

In Ambohitantely Special Reserve the grasslands and low-lying marsh valleys support a dense insect population of grasshoppers (*Nomadacris septemfasciata*) and provide habitat for snakes and savannah birds. Grasshoppers were the predominant prey taken by frequency, but in terms of biomass birds, reptiles, and mammals made up 90% of the harrier diet.

The Madagascar Harrier is categorized as a vulnerable species (BirdLife International 2000). In Ambohitantely Special Reserve, and most likely throughout Madagascar, there are three major hu-

man-caused threats toward this species. First, adults are persecuted for food and as a threat to domestic fowl. In one case in 1996, Randriamanga (2000) met a poacher who had displayed carcasses of 13 Madagascar Harriers he had killed. Local people also consume the eggs and nestlings as a source of protein (Randriamanga 2000). Second, during every dry season (April–October) the grasslands of Madagascar, especially the high-plateau region which includes the reserve, are burned by human-set fires to stimulate green growth for cattle fodder and land clearing. During this study, two harrier nests were destroyed during the incubation period by uncontrolled human set fires. In 1996, in an area near Ambohitantely, Paverne (1997) suggested a wild fire destroyed one of the harrier nests he was observing. Finally, the conversion of low-lying marshes and wetlands to rice fields for human food production reduces nesting habitat for this species. Currently, the vulnerable status of the Madagascar Harrier is justified based on threats to its habitat and its sparse distribution throughout Madagascar. This species has been recorded at a number of protected areas and national parks, but most of the protected areas have been established to preserve forested habitat and have limited grassland and wetland protection. Biologists need more information on the Madagascar Harrier population size and dynamics in order to provide conservation strategies and protect it in the future.

ACKNOWLEDGMENTS

This study was conducted by The Peregrine Fund's Madagascar Project with funding provided, in part, by John D. and Catherine T. MacArthur Foundation, the Walt Disney Company Foundation, the Little Family Foundation, Environment Now and other important contributions. We thank Richard Ranarisoa, Director of Association Nationale pour la Gestion des Aires Protégées at Ambohitantely Special Reserve and his staff for their support during this study, and Steve Goodman of WWF for his assistance in identifying prey remains. We also thank the Direction des Eaux et Forêts for their collaboration with the Peregrine Fund's Project in Madagascar. We especially thank R. Watson and B. Burnham for their continued support of this project and L. Kiff, J. Berkelman, R. Simmons, V. Bretagnolle, and J. Bednarz for their comments and improving an earlier version of this manuscript and Amy Siedenstrang for creating the map.

LITERATURE CITED

- BIRDLIFE INTERNATIONAL. 2000. Threatened birds of the world. Lynx Edicions and BirdLife International, Barcelona and Cambridge, U.K.
- BRETAGNOLLE, V., J.M. THIOLLAY, AND C. ATTIE. 2000. Status of Réunion Marsh Harrier (*Circus maillardi*) on

- Réunion Island. Pages 669–776 in R.D. Chancellor and B.-U. Meyburg [EDS.], *Raptors at risk*. World Working Group on Birds of Prey and Owls. Hancock House, Berlin, Germany.
- DUNNING, J.B., JR. 1993. *CRC handbook of avian body masses*. CRC Press Inc., Boca Raton, FL U.S.A.
- GARBUTT, N. 1999. *Mammals of Madagascar*. Yale University Press, New Haven, CT U.S.A.
- GARGETT, V. 1990. *The Black Eagle, a study*. Acorn Books and Russell Friedman, Johannesburg, South Africa.
- DEL HOYO, J., A. ELLIOTT, AND J. SARGATAL (EDS.). 1994. *Handbook of the birds of the world*. Vol. 2. New world vultures to guineafowl. Lynx Edicions, Barcelona, Spain.
- LANGRAND, O. 1990. *Guide to the birds of Madagascar*. Yale University Press, New Haven, CT U.S.A.
- . 1995. *The effects of forest fragmentation on bird species in Madagascar: a case study from Ambohitantely Forest Reserve on the Central High Plateau*. M.S. thesis, Univ. of Natal, Durban, South Africa.
- MEYBURG, B.-U. 1974. Sibling aggression and mortality among nestling eagles. *Ibis* 116:224–228.
- NICOLL, M. AND O. LANGRAND. 1989. *Madagascar: revue de la conservation et des aires Protégées*. World Wide Fund for Nature International, Gland, Switzerland.
- PAVERNE, L. 1997. Nidification et comportement de busard de maillard (*Circus maillardi*) dans la région d'Ankazobe au nord-ouest d'Antananarivo. *Working Group on Birds in the Madagascar Region Newsletter* 7:21–24.
- RAND, A.L. 1936. The distribution and habits of Madagascar birds. *Bull. Am. Mus. Nat. Hist.* 72:143–499.
- RANDRIAMANGA, I. 2000. Contribution à l'étude de la biologie de la reproduction et écologie de busard de Madagascar *Circus macroscels* dans le tampoketsa d'Ankazobe. Mémoire de D.E.A., Université d'Antananarivo, Antananarivo, Madagascar.
- SIMMONS, R.E. 1988. Offspring quality and the evolution of cannibalism. *Ibis* 130:339–357.
- . 2000. *Harriers of the world: their behaviour and ecology*. Oxford Univ. Press, Oxford, U.K.
- THORSTROM, R. 1996. Methods for capturing tropical forest birds of prey. *Wildl. Soc. Bull.* 24:516–520.
- AND L.A. RENE DE ROLAND. 2000. Status and conservation of raptors on the Masoala Peninsula. Pages 35–41 in R.D. Chancellor and B.-U. Meyburg [EDS.], *Raptors at risk*. World Working Group on Birds of Prey and Owls. Hancock House, Berlin, Germany.

Received 29 July 2003; accepted 16 May 2004

BREEDING BIOLOGY OF THE GREY-FACED BUZZARD (*BUTASTUR INDICUS*) IN NORTHEASTERN CHINA

WEN-HONG DENG¹

MOE Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences,
Beijing Normal University, Beijing, 100875 China

WEI GAO

College of Life Sciences, Northeast Normal University, Changchun, 130024 China

JIANG ZHAO

College of Life Sciences, Jilin Normal University, Siping, 136000 China

ABSTRACT.—We studied the breeding biology of the Grey-faced Buzzard (*Butastur indicus*) in Zuojia Nature Reserve, Jinlin province, China from 1996–98. Grey-faced Buzzards are summer residents in northeastern China. Nesting sites were occupied in March and annual reoccupancy was 60%. Grey-faced Buzzards built new or repaired old nests in late March and laid eggs in early April. Laying peaked in late April and spanned 32 d ($N = 15$ clutches). Clutches consisted of 3–4 eggs, incubated for 33 ± 1 d predominantly by the female, to whom the male brought prey. After young hatched, the female also began hunting. The mean brood-rearing period was 38 ± 2 d and nestling females attained larger asymptotic mass than males, but the latter grew faster. Males fledged at a mean age of 35 d and females at 39 d. Young were slightly heavier than adults at fledging, but the wing chord and tail lengths were shorter than those of adults. A total of 50 eggs was laid in 15 nests (\bar{x} clutch size = 3.3), of which 80% hatched and 90% of the nestlings fledged. A mean of 2.4 young fledged per breeding attempt. Overall nest success was 80%. Causes of nest failure were addled eggs and predation on eggs or nestlings by small mammals (e.g., Siberian weasel [*Mustela siberica*]).

KEY WORDS: Grey-faced Buzzard; *Butastur indicus*; breeding biology; clutch size; nestlings; fledglings; development; reproductive success.

BIOLOGÍA REPRODUCTIVA DE *BUTASTUR INDICUS* EN EL NORESTE DE CHINA

RESUMEN.—Estudiamos la biología reproductiva de *Butastur indicus* en la reserva Natural de la Provincia de Jinlin en China desde 1996–98. *B. indicus* es un residente de verano en el noreste de China. Los sitios de anidación fueron ocupados en Marzo y la reocupación anual de los nidos fue el 60%. *B. indicus* construyó o reparó los nidos viejos a finales de Marzo y puso huevos a principios de Abril. El pico de la postura ocurrió en Abril y abarcó 32 días ($N = 15$ nidadas). Las nidadas fueron de 3–4 huevos incubados 33 ± 1 días, los cuales fueron incubados predominantemente por la hembra, a la cual el macho traía presas. La media del periodo de crecimiento fue de 38 ± 2 días, las hembras obtuvieron una mayor masa corporal que los machos, pero estos crecieron más rápidamente. Los machos emplumaron en un promedio de 35 días y las hembras a los 39 días. Los juveniles al emplumar fueron levemente más pesados que los adultos. Una media de 50 huevos fue obtenida en 15 nidos (tamaño de la nidada = 3.3), de los cuales un 80% eclosionaron y un 90% de los pichones emplumaron una media de 2.4 pichones emplumados por intento reproductivo. El éxito general de anidación fue de 80%. Las causas del fracaso de anidación fueron atribuibles a huevos podridos y a la depredación de pichones por pequeños mamíferos (*Mustela siberica*).

[Traducción de César Márquez]

Among subtropical birds, raptors are one of the least-studied groups, and relatively little is known

about their breeding biology, particularly in China. Since 1995, several surveys have been conducted to document the distribution and population status of Grey-faced Buzzards (*Butastur indicus*) during

¹ E-mail address: dengwh@bnu.edu.cn



Figure 1. The distribution of the Grey-faced Buzzard. Dark shading indicates breeding range; grey shading indicates winter ranges. The white square indicates the study area.

their breeding season in Zuojia Nature Reserve, northeastern China. Because of these survey efforts, the species is known from more localities than ever before in China (Deng et al. 1997). Feng et al. (1991) estimated the population at a maximum of 30 breeding pairs in Zuojia Nature Reserve and 1000 breeding pairs in northeastern China. The species occurs either in conifer forests, broad-leaf forests, or mixed forests. Grey-faced Buzzards are summer residents in this area. A variety of reports suggest that most Grey-faced Buzzards that breed in northeastern China migrate to Okinawa, Taiwan, the Philippines, Indonesia, and Malaysia for wintering (Ching et al. 1989, Severinghaus 1991, Deng et al. 2003).

Until now only two cases of breeding by Grey-faced Buzzards have been reported in China (Feng et al. 1991, Zheng and Wang 1998), and these only included brief descriptions. The nests and eggs have been described (Cheng 1987, Xu 1995), and breeding territory and roost characteristics have been reported (Kojima 1982, Deng et al. 1997, 2003). Here, we describe breeding biology of Grey-faced Buzzards based on 3 yr of observations in Zuojia Nature Reserve in northeastern China.

STUDY AREA

The study area, ca. 184 km² in size, was located in Zuojia Nature Reserve and included the Tumengling Mountains and Zhujia Mountains ranging from the eastern Changbai Mountains to the western plain (126°1'–127°2'N, 44°6'–45°5'E; Fig. 1). Elevation at the site ranged from 200–500 m above sea level. The climate is east monsoon, characterized by hot, dry summers and cold, snowy winters. Mean monthly temperatures ranged from –20.5°C in January to 23.6°C in August during

study period. The vegetation within the study area was quite diverse, although the forest type was secondary forest. The seven tree species mainly present on the study area were Mongolian oak (*Quercus mongolica*), Dahurian birch (*Betula davurica*), Manchurian linden (*Tilia mandshurica*), Japanese elm (*Ulmus japonica*), Scotch pine (*Pinus sylvestris*), Korean larch (*Pinus koraiensis*), and Masson pine (*Pinus massoniana*; Deng et al. 1997). In the study area, Dahurian rose (*Rosa dahurica*), Korean rose (*Rosa doreana*), willowleaf spiraea (*Spiraea salicifolia*), ural false-spiraea (*Sorbaria sorbifolia*), and Sakhalin honeysuckle (*Lonicera maximowiczii*) dominated the shrub layer.

METHODS

Breeding areas were surveyed by foot periodically throughout the breeding season to find mated pairs. We defined nesting sites as an area where aerial displaying, mating, nest-building, incubating, brooding, and repeated prey-carrying occurred. An area with a mated pair was considered an occupied nesting site. Observations of Grey-faced Buzzards in their breeding areas were made from above canopy lookouts and ground blinds with the aid of 8–12× binoculars and a spotting scope. We distinguished mature males, females, and immatures by their body size and plumage color (Deng 1998). The body size of males was smaller than that of females. Also, the plumage color of adults was darker than that of immatures. We classified display flight as territorial only if followed by an encounter between the resident and an intruder (Delannoy and Cruz 1988), otherwise interactions between pair members were considered courtship. We estimated above-ground heights of flying birds in courtship relative to known above-ground heights of hills and other topographic features. Nest measurements were taken at accessible nests. Nest height was measured in plumb-line distance from the nest to ground level. Shortest diameter, longest nest diameter, nest depth exterior, and nest depth interior were measured using a ruler.

We measured egg dimensions (breadth and length to the nearest 0.1 mm) with vernier calipers, and determined egg mass and body mass of nestlings (nearest 0.1 g) with a spring scale (Pesola, Barr, Switzerland). Individual young were marked with colored leg bands soon after hatching. Ricklefs' (1967) method of fitting equations to growth curves was used to compare growth patterns of male and female nestlings. Nestlings were weighed, and the length of their wing chord, tail length, culmen, and tarsal length were measured at 3-d intervals. After fledging, mist nets were used to capture fledglings and adults, which were measured (tarsal length, wing chord, culmen, and tail length) and weighed. Tarsal length was measured from the intertarsal joint to the bend of the foot. The tail length (mm) was measured from the base to the tip of the center rectrix. Reproductive output was the total number of fledglings produced over a nestling season. Reproductive success was a general term that included several measures and components, expressed on per pair, per breeding attempt, or per egg basis. All statistical procedures followed Zar (1999).

RESULTS

Courtship and Territoriality. We observed the movements and behavior of fledglings for 118 hr

Table 1. Grey-faced Buzzard nest-site characteristics in northeastern China.

NEST-SITE CHARACTERISTICS	MEAN	SD	RANGE	N
Nest height (m)	13.3	3.5	8.8–16.6	15
Nest-tree height (m)	17.5	3.3	13.5–22.9	15
Nest tree DBH (cm)	30.8	9.3	22.1–44.2	15
Shortest nest diameter (cm)	30.3	6.2	25.5–38.6	13
Longest nest diameter (cm)	35.1	7.6	28.9–40.3	13
Nest depth exterior (cm)	42.6	11.5	33.7–55.6	13
Nest depth interior (cm)	17.3	8.1	9.8–29.5	13
Nest support branch diameter (cm)	8.6	3.7	5–18	10

at two nests. Grey-faced Buzzards are summer residents that establish nesting territories only during the breeding season in northeastern China. Reoccupancy of nesting sites occurs in early March. Annual reoccupancy was 60% ($N = 15$). Six nests were reoccupied at least twice. Most Grey-faced Buzzard activity during March and early April involved courtship and territorial display flights. A typical courtship flight began when the male circled above the nest site and the female followed shortly afterwards. Both male and female soared and actively flew giving intermittent vocalizations. Males used flapping more frequently than females and circled in the sky higher than the females. Buzzards reached estimated above-ground heights of 30–150 m ($\bar{x} = 80$ m, $N = 12$). Display bouts lasted 5–20 min ($\bar{x} = 14$ min, $N = 12$). Most courtship flights (75%, $N = 12$) ended with a steep dive into the forests. We observed 11 territorial display flights in the study area in 1998. Resident males initiated territorial behavior from a perch ($N = 7$) or while in flight ($N = 4$). When intruders entered air space near the nesting site, resident males flew straight at them and evicted intruders. Buzzards only chased raptors and relatively large birds such as corvids.

Nest Building and Nest Characteristics. Grey-faced Buzzards started nest building shortly after occupying their nesting areas in late March or early April. Both adults took part in nest construction. In 1997, during 80 hr of observation at three nests, we observed deliveries of 72 dry sticks; males contributed 43 (60%) and females 29 (40%). Most nest building activity occurred between 0600–0730 H. Nests were built in trees on forked branches. Buzzards gathered dry sticks from the ground or nearby trees within 50 m of the nest trees. Several nests contained dried or green needles of *Pinus* spp. in the nest platform. Near nest completion,

the pair created a bowl by compacting a layer of finer twigs with their talons and breast. The earliest nest-building activity in a season was observed on 21 March 1998. The earliest copulation was observed on 29 March 1997, ca. 4 wk before laying. Copulation usually occurred after a courtship display.

More than half ($N = 8$) of nests were located in Korean larches. Nests typically were placed in the upper half (\bar{x} height = 13.3 m) of relatively tall trees (\bar{x} height = 17.5 m; Table 1).

Egg Laying, Incubation, and Hatching. By late April, females remained near the nest site and were mostly inactive. Males provided food at this stage and during the following months. Earliest recorded laying dates were 20 April 1996, 17 April 1997, and 19 April 1998. Laying of first clutches spanned 37 d (17 April–24 May). First clutches were on average completed on 12 April \pm 9 d (mean \pm SD, $N = 15$ clutches) for 3 yr. Mean clutch size was 2.9 ± 0.8 ($N = 15$). Mean egg dimensions were 53.7×43.3 mm ($N = 47$). The mean egg mass was 51.5 g (49.8–53.5 g, $N = 47$), 9.9% of the female's body mass (\bar{x} female body mass = 490 g, $N = 6$) and 38.2% of her mass for a clutch of four eggs.

Females incubated while males provided food. In 1997, we recorded incubation patterns of a female during 12-hr periods (0600–1800 H) for 5 consecutive days. The female incubated 22% of the first day (1 egg), 29% of the second day (2 eggs), 38% of the third day (3 eggs), 39% of the fourth day (3 eggs), and 43% of the fifth day (4 eggs). Most hatching occurred during late May, except when pairs renested. Hatching was asynchronous, spanning 1–3 d. Hatching for all years peaked on 25 May \pm 4 d and spanned 12 d (20 May–2 June, $N = 10$). The incubation period from laying to

hatching of the last egg averaged 33.5 ± 1.6 d ($N = 9$).

Nestling Period. Young emerged from eggs with eyes closed. The eyes began to open after 0.5 d. By the fourth day after hatching, the young could stand up and showed improved coordination in pecking at food held above them by the female. Nestlings could be sexed accurately in the nest after they were 8 d old by examining the feather tips (the primary feather tips of males emerged from the sheaths at ca. 8 d, $N = 14$; females at 9–10 d, $N = 12$) and extent of black in wing (males had more black than females). The first tail feathers appeared at approximately 12.5 d in males ($N = 14$) and 12 d in females ($N = 12$). Young began to replace the natal quill-coverts down 20 d after hatching.

During the nestling period, males hunted more frequently than females. However, only females dismembered and fed prey to young. Late in the third week and early in the fourth week after hatching (19–26 d), females spent less time brooding. In one nest, the female brooded four 18-d-old young more than half of the time ($N = 8$ hr), but decreased brooding to 8% ($N = 8$ hr) when the young were 26 d old. From 25–31 d after hatching, the young squabbled over prey and were able to dismember most soft parts. At 26–28 d, the young flapped their wings regularly and began to roost overnight in branches near the nests. The nestling period ended when the young flew short distances from the nest and roosted in trees 10–20 m away. Nine males fledged at a mean of 35 d of age (range = 33–38, $SD = 1.2$), and 10 females at 39 d (range = 37–41, $SD = 1.1$), with a combined mean fledging age of 37 d (range = 31–41, $SD = 2$).

Growth Rate. Increase in tarsi length, mass, wing and tail length followed Gompertz or logistic growth patterns (Fig. 2). Male and female nestlings showed differences in mass growth patterns. Females attained a higher asymptotic mass than males (\bar{x} female = 559 g, $N = 10$; \bar{x} male = 462 g, $N = 9$). It took males 12.6 d to grow half their asymptotic mass, but 15.1 d for females. The time interval of growth from 10–90% of the asymptote (t_{10} – t_{90}) was shorter in males than in females (\bar{x} male = 25 d, $N = 9$; \bar{x} female = 27 d, $N = 10$). Males generally fledged earlier (36–38 d) than females (37–41 d). Both males and females at fledging were slightly heavier than adults (adult mass: \bar{x} male = 396 ± 11 g, $N = 9$; \bar{x} female = 519 ± 13 g, $N = 10$).

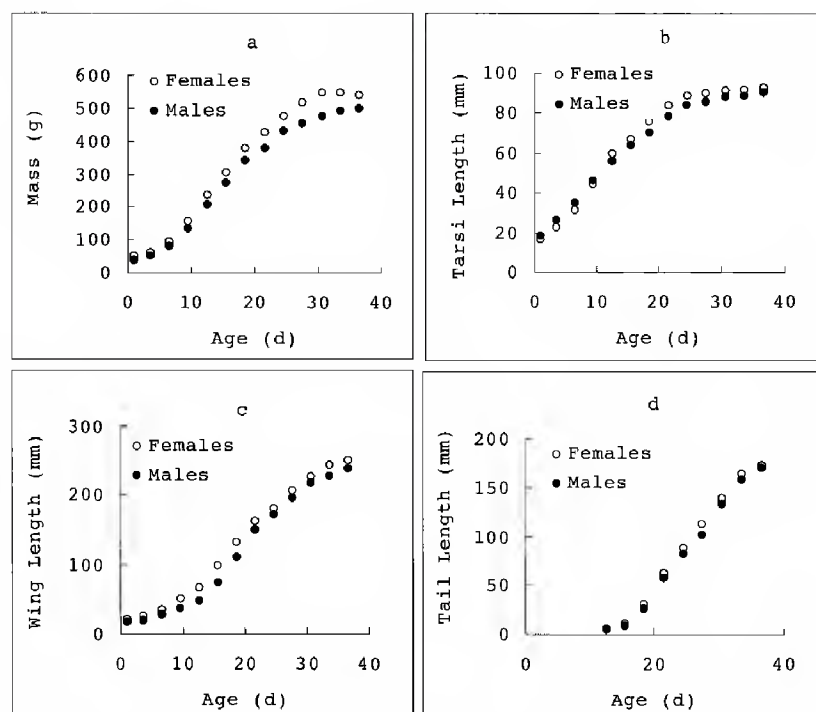


Figure 2. Changes of mass (a) tarsus length (b) wing chord length (c) and tail length (d) of males ($N = 9$) and females ($N = 10$) of Grey-faced Buzzard nestlings in northeastern China.

Fledgling and Post-fledgling Periods. Fledging spanned nearly 7 wk, from mid-June–late July. After fledging, young remained in the nest area and returned to the nest frequently. By 42–48 d after hatching, the young had dispersed 50–100 m from the nest. Adult females still fed young at this time. The young were capable of handling and carrying prey to a perch away from the nest and their siblings. Young constantly solicited food and mobbed adults when the adults entered the nest area.

At two nest sites, we monitored movements of five young. One young did not spend time in the nest area away from the nest, but dispersed abruptly. Four spent 2 d away before their dispersal. The ages of young at one nest site averaged 76 d ($N = 3$) and in another 80 d ($N = 2$) when they dispersed. Adults and young did not stay together after the latter dispersed.

Reproductive Success. From 1996–98, 18 nests were built and 15 nesting attempts were observed (eggs laid; Table 2). In 15 nesting attempts, two nest failures occurred during incubation and one during the nestling stage. According to our observations, the causes for nest failure ($N = 5$) were predation on eggs or nestlings by small mammals (such as the Siberian weasel [*Mustela siberica*]).

DISCUSSION

Our observation of Grey-faced Buzzard courtship and territorial behavior appears to differ from

Table 2. Annual reproductive success of Grey-faced Buzzards during breeding season (1996–98) at Zuojia Nature Reserve, northeastern China.

YEAR	NESTING ATTEMPTS ^a	EGGS LAID	MEAN CLUTCH SIZE	EGGS HATCHED (%)	YOUNG FLEDGED (%)	SUCCESSFUL NESTS <i>N</i> (%)	PRODUC- TIVITY PER NEST ATTEMPT
1996	4	12	3.0	10 (83)	8 (80)	4 (100)	2.0
1997	6	22	3.7	15 (68)	14 (93)	4 (67)	2.3
1998	5	16	3.2	14 (87)	14 (100)	4 (80)	2.8
Total	15	50	3.3	40 (80)	36 (90)	12 (80)	2.4

^a Number of nests with eggs.

other *Butastur* buzzards. White-eyed Buzzards (*B. teesa*) and Rufous-winged Buzzards (*B. liventer*) seldom circled above their nest site during the pre-nesting period (Smythies 1986, Cheng 1987, Xu 1995). Grasshopper Buzzards (*B. rufipennis*), which occurs in Africa, performed soaring displays above the nest site (Rasa 1987, Thiollay and Clobert 1990). The behavior of Grey-faced Buzzards circling above the nest site during the pairing period might serve both to attract potential mates and to give an assertive message to potential intruders. Grey-faced Buzzards showed strong territorial behavior when birds of similar size and shape entered the territory. We frequently observed chasing behaviors of the buzzards directed toward congeners, other raptors, waterfowl, and corvids.

The nesting period was ca. 105 d from nest building to dispersal of young from their natal areas. This is comparable to White-eyed and Rufous-winged buzzards, which have relatively short nesting periods (Smythies 1986, Cheng 1987, Xu 1995, Gao 2003). Also, the breeding period in Grey-faced Buzzards is shorter than that of their tropical counterparts of comparable size (Newton 1979, Mader 1981, Delannoy and Cruz 1988, Thorstrom and Quixchán 2000). The nesting cycle of songbirds also is longer in tropical than in temperate regions. Differences between tropical and temperate avian groups are due to differences in the length of time required to complete various stages of breeding (Newton and Marquiss 1982, Delannoy and Cruz 1988). The shorter breeding period of the Grey-faced Buzzards compared to that of the White-eyed and Rufous-winged buzzards (Smythies 1986, Cheng 1987, Xu 1995) resulted from shorter periods of nest building, courtship, egg laying, and brood rearing. White-eyed and Rufous-winged buzzards built their nests earlier than the Grey-faced

Buzzards and they had a relatively longer brood-rearing period (Cheng 1987, Xu 1995).

It is possible that the breeding season, especially the laying and nestling period of the Grey-faced Buzzard, was restricted by food abundance. In northeastern China, the prey of the buzzards are mainly frogs, reptiles (snakes and lizards), rodents, and some small birds (Deng 1998). We suggest that the nestling and fledging periods in Grey-faced Buzzards were synchronized with the peak of prey abundance.

Grey-faced Buzzards preferred to build their nests in large Korean larches and Scotch pines with high canopy closure in wooded areas (Deng et al. 2003). This selection was different from that of White-eyed and Rufous-winged buzzards (Xu 1995, Deng et al. 2003). White-eyed Buzzards usually built their nests in broadleaf tree species in open country or cultivated areas (Cheng 1987). However, Rufous-winged Buzzards preferred to build their nests in conifer or broadleaf tree species near rivers and swamps in lowland plains (Smythies 1986, Lekagul and Round 1991).

Most raptors select habitat types with relatively open canopy for easier access to nests, and fewer connections between neighboring trees, which limits the movements of arboreal animals (e.g., Moore and Henny 1983, Cerasoli and Penteriani 1996, Malan and Robinson 2001, Malan and Shultz 2002). We did not find this selection pattern in our study. On the contrary, Grey-faced Buzzards selected their breeding habitat in dense conifer or mixed forests. Thorstrom and Quixchán (2000) suggested that dense forest habitat may limit raptor hunting behaviors. According to our observations, Grey-faced Buzzards seldom hunt in the forest near nest sites. Their foraging sites were often in open

areas such as pastures, peat bogs, and paddy fields near the nest sites.

Female nestlings attained a higher asymptotic mass than males. However, males left the nests earlier than females. Sexual differences in growth rates have been found in other raptors (e.g., Schnell 1958, Moss 1979, Delannoy and Cruz 1988).

In this study, during the late nestling period, young were slightly heavier than adults, and the mass decreased slightly at least for females when the fledgling period began (Fig. 2). This pattern also was found in the Common Buzzard (*B. buteo*; Xu 1995) and the Upland Buzzard (*Buteo hemilasius*; Gao 2003). Grey-faced Buzzard young fledged (took their first flight from the nest tree) 31–41 d after hatching. This is comparable to the Rufous-winged Buzzard's relatively short brood-rearing period (Gao 2003).

Productivity seemed high during the study, with 2.4 young fledged per breeding attempt. High productivity was the result of a low nest predation rate and high nesting success (80%). In our study, causes of nest failure were addled eggs ($N = 9$) and predation on eggs or nestlings ($N = 8$) by mammals such as the Siberian weasel. The richness and density of animals that prey on Grey-faced Buzzards was low in the study area (Deng 1998). Few mortalities were observed in either adults or young. For example, two adult females banded in 1996 were still on their territories in 1998. Thus, if a pair of Grey-faced Buzzards was successful in laying eggs, they had a good chance of producing offspring successfully.

There are no data for productivity of other *Buteo* species. However, productivity and nesting success was higher for the Grey-faced Buzzard than for the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus*; Delannoy and Cruz 1988), and the Bicolored Hawk (*Accipiter bicolor*; Thorstrom and Quixchán 2000). Sharp-shinned Hawks suffered a higher degree of nest failures from nestling mortality attributed to parasite infestation and clutch desertion. Bicolored Hawks laid addled eggs and suffered predation on eggs or nestlings. These patterns were consistent with the general trend that tropical birds have lower fecundity and reproductive success than their counterparts in temperate latitudes (Ricklefs 1969, Newton 1979).

ACKNOWLEDGMENTS

We thank Liu Yang, Yan-hui Li, Ren-kai Song, Lu-ye Tang, and Ya-mei Yu for help in the field. Wei-dong Luo

and Bao-xue Zhang were very patient in helping with data collection. Earlier drafts of this manuscript were improved by comments from Zheng-wang Zhang and Yan-yun Zhang. The staff of Zuojia Natural Protection Area provided logistical support during the study period. We also thank the anonymous reviewers of The Journal of Raptor Research.

LITERATURE CITED

- BORTOLOTTI, G.R. 1986. Evolution of growth rates in eagles: sibling competition vs. energy considerations. *Ecology* 67:182–194.
- CERASOLI, M. AND V. PENTERIANI. 1996. Nest-site and aerial point selection by Common Buzzards (*Buteo buteo*) in central Italy. *J. Raptor Res.* 30:130–135.
- CHENG, T. 1987. A synopsis of the avifauna of China. Science Press, Beijing, China.
- CHING, H.C., S.T. YU, AND C.H. CHIANG. 1989. A survey of Grey-faced Buzzard Eagle hunting in ManChou Area. Kenting National Park, Taipei, China.
- DELANNOY, C.A. AND A. CRUZ. 1988. Breeding biology of the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*). *Auk* 105:649–662.
- DENG, W.H. 1998. Breeding ecology and habitat characteristics of Grey-faced Buzzard. M.S. thesis, Northeast Normal Univ., Changchun, China.
- , W. GAO, AND G.M. ZHENG. 2003. Nest and roost habitat characteristics of the Grey-faced Buzzard in northeastern China. *J. Raptor Res.* 37:228–235.
- , X. WANG, AND W. GAO. 1997. Breeding habitat selection of the Grey-faced Buzzard Eagle. *J. Northeast Norm. Univ.* 9:57–61.
- FENG, H.L., G.Q. XIANG, AND K.Q. ZHANG. 1991. Observation on breeding Grey-faced Buzzard Eagle. Chinese Science Publishing House, Beijing, China.
- GAO, W. 2003. Ecology of falcon order in China. Chinese Science Press, Beijing, China.
- KOJIMA, Y. 1982. Territory and territorial behavior of the Grey-faced Buzzard Eagle *Buteo indicus*. *Tori Bull. Ornithol. Soc. Jpn.* 30:117–147.
- LEKAGUL, B. AND P.D. ROUND. 1991. A guide to the birds of Thailand. Saha Barn Bhaet, Bangkok, Thailand.
- MADER, W.J. 1981. Notes on nesting raptors in the llanos of Venezuela. *Condor* 83:48–51.
- MAIAN, G. AND E.R. ROBINSON. 2001. Nest-site selection by Black Sparrowhawks *Accipiter melanoleucus*: implications for managing exotic pulpwood and sawlog forests in South Africa. *Environ. Manage.* 28:195–205.
- AND S. SIIULTZ. 2002. Nest-site selection of the Crowned Hawk-Eagle in the forests of Kwazulu-natal, South Africa, and Tai, Ivory coast. *J. Raptor Res.* 36:300–308.
- MOORE, K.R. AND C.J. HENNY. 1983. Nest site characteristics of three coexisting accipiter hawks in northeast Oregon. *Raptor Res.* 17:65–76.
- MOSS, D. 1979. Growth of nestling Eurasian Sparrowhawks, *Accipiter nisus*. *J. Zool.* 197:297–314.

- NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.
- AND M. MARQUISS. 1982. Fidelity to breeding area and mate in Eurasian Sparrowhawks, *Accipiter nisus*. *J. Anim. Ecol.* 5:327–341.
- RASA, O.A.E. 1987. Patterns of intra-African small raptors spring migration in the Taru Desert, Kenya. *Afr. J. Ecol.* 25:165–171.
- RICKLEFS, R.E. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48:978–983.
- . 1969. The nesting cycle of songbirds in tropical and temperate regions. *Living Bird* 8:165–175.
- SCHNELL, J.H. 1958. Nesting behavior and food habitats of goshawks in the Sierra Nevada of California. *Condor* 60:377–403.
- SEVERINGHAUS, L.L. 1991. The status and conservation of Grey-faced Buzzard-Eagles and Brown Shrikes migrating through Taiwan. Pages 203–223 in T. Salathé [ED.], Conservation migratory birds. ICBP Technical Publication, Bros. Ltd, London, U.K.
- SMYTHIES, B.E. 1986. The birds of Burma. Nimrod Press, Hants, U.K.
- THIOLLIAY, J.M. AND J. CLOBERT. 1990. Comparative foraging adaptations of small raptors in dense African savanna. *Ibis* 132:42–57.
- THORSTROM, R. AND A. QUIXCHÁN. 2000. Breeding biology and nest site characteristics of the Bicolored Hawk in Guatemala. *Wilson Bull.* 112:195–202.
- XU, W.S. 1995. Chinese raptors. Chinese Science Press, Beijing, China.
- ZAR, J.H. 1999. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ U.S.A.
- ZHENG, G.M. AND Q.S. WANG. 1998. China red data book of endangered animals. Chinese Science Press, Beijing, China.

Received 20 August 2003; accepted 15 May 2004

Associate Editor: Marco Restani

SHORT COMMUNICATIONS

J Raptor Res. 38(3):270–275

© 2004 The Raptor Research Foundation, Inc.

VARIABLE RETENTION TIMES FOR RECTRICES AT DIFFERENT LOCI IN A GOLDEN EAGLE

DAVID H. ELLIS¹

USGS Southwest Biological Science Center, Sonoran Desert Research Station, HC 1 Box 4420, Oracle, AZ 85623 U.S.A.

MARC KÉRY

Swiss Ornithological Institute, CH—6204 Sempach, Switzerland

KEY WORDS: *Golden Eagle*, *Aquila chrysaetos*; *molt*; *plumage*.

Perhaps the most obvious feature in the plumage of non-juvenile Golden Eagles (*Aquila chrysaetos*) is the presence of feathers from more than 1 year (Sushkin 1900, Tjernberg 1977, Bloom and Clark 2001). Even captive birds in good health, fed *ad libitum*, do not completely molt each yr (Jollie 1947). It is normal for all (or nearly all) head feathers to be of a single generation (all molted in one season; Ellis unpubl. data). Elsewhere on the body, conspicuously faded feathers lie interspersed with freshly grown feathers even in winter when contour molt has ceased (however, winter molt of a few feathers is not uncommon; Watson 1997, Bloom and Clark 2001, Ellis unpubl. data).

A minor focus in Jollie's (1947) detailed study of molt in the Golden Eagle was rectrix replacement rate. Decades later, Servheen (1976) compared Jollie's data for tail molt of one bird with his own data for two other Golden Eagles. From that treatment, Servheen concluded that center rectrices (loci R1 and L1) never molted less than 35 d apart and R1 is always molted before L1. Unfortunately, both of these studies involved only 1 or 2 yr of data.

Although the scientific literature is awash in articles on avian molt, most of these deal with either the hormone control of molt or they provide data based on one-time examination of many birds. After his extensive treatment of Golden Eagle molt based mostly on captive birds, Jollie (1947) stated: "The tail feathers have lost all semblance to order and irregularities are the rule. . . ." Here, we seek to define order in tail molt by identifying consistent patterns. Our data derive from a continuous 15-yr period for one Golden Eagle and short term observations of two other captive birds.

METHODS

We primarily monitored one adult female Golden Eagle (ca. 22-yr old when obtained from the Red Lodge Zoo, Montana; 45°N, 109°W). This bird was reportedly obtained as a nestling in Montana, was well adjusted to captivity, was received in October 1983, and laid eggs for many years. She was held for 2 yr near Oracle, AZ (32°N, 110°W), then held for 10 yr at two locations (39°N, 77°W and 38°N, 76°W) in the vicinity of Washington, DC. In 1995, she was returned to Oracle, AZ where she remains. The bird was held in outdoor facilities, where she was subject to local light and temperature regimes. During each molt season, the eagle had free range of one of six flight pens (3–7 m wide, 5–12 m long, and 2–3 m high).

Here, we describe her tail molt from 1984–98 inclusively. The value of our study lies in what it suggests about wild eagles and, to a lesser degree, about wild birds of other species. Obviously, this study could not have been performed with wild birds. In wild birds, propensity to molt is governed by body condition, hence by food intake. Whereas in captivity, the variables related to hunger level and body condition can be standardized by feeding *ad libitum*.

Our study then is a description of molt, not influenced by the variable of body condition. Our subject bird was normally fed once a day to satiation. Throughout the study, the bird was in good health as indicated by her well-formed feathers that showed normal coloration, and typically had very few "fault bars" (Grubb 1989). Second, the plumage in this eagle was much less worn and less faded than for wild adult eagles (museum specimens [pers. obs.] and adults observed at nests [Ellis 1979]). Third, the eagle flew well when flown free.

We inscribed on the calamus the date when each feather was dropped. Normally, we collected feathers on the same day they fell. We also refer to the tail molt in two other captive birds. We have five seasons of molt data for a bird taken as a nestling in July 1954 at Kluane Lake, Yukon Territory, Canada. These data were collected by a well-known raptorophile, the late Dr. Walter Spofford. For the second eagle, taken as a nestling in 1973 in Montana, we have three molt-years of data.

DATA ANALYSIS

We recorded feather-retention times in year and in month (to the nearest 0.5 mo). We did not record exact

¹ Present address: Institute for Raptor Studies, HC 1 Box 4420, Oracle, AZ 85623 U.S.A.; e-mail address: dcellis@theriver.com

Table 1. Rectrix replacement history for an adult female Golden Eagle over a 15-yr period.

LOCUS	YEAR WHEN RECTRIX WAS REPLACED															\bar{X} DURATION ^a
	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	
L6	X		X	X		X		X		X		X		X		1.8
L5	X		X		X		X		X		X		X		X	2.0
L4	X		X		X			X			X		X			2.4
L3	X			X		X		X		X			X		X	2.3
L2	X		X		X		X		X		X			X		2.2
L1	X	X		X	X	X		X		X		X		X		1.6
R1	X		X		X		X		X		X		X		X	2.0
R2	X	X		X		X		X		X		X			X	2.0
R3	X		X		X		X		X		X			X		2.0
R4	X			X		X		X			X		X			2.2
R5	X		X		X		X		X		X		X		X	2.0
R6	X		X	X		X		X		X		X		X		1.9
Total lost	12	2	8	6	7	6	5	7	5	5	7	4	6	5	5	

^a The mean retention time (arithmetic mean) for 14 potential molt seasons (for loci where a rectrix was lost in 1998) or for 12 or 13 potential molt seasons for feathers last replaced in 1996 or 1997.

molt dates for the first-molt year (1984) and for two other feathers, so we were able to measure retention times to the next molt for these 14 feathers only as the number of years. As a result, we have more, but coarser, data (78 retention times) based on yearly records, while for the monthly data, we have a more precise measure but fewer (64) retention times. All analyses were conducted both on yearly and monthly data. Results were similar so we present the statistical analyses only for the monthly data.

We analyzed the effect of side (left-right) and locus (rectrix position 1–6) on the intervals between molt of successive rectrices with a 2-way, fixed-effects, analysis of variance. We partitioned the locus factor into orthogonal-polynomial contrasts to test our hypothesis that feathers at mid-span loci at each side (i.e., loci 3, 4) are retained longer than those of loci 1, 2, 5, or 6. A significant-quadratic locus contrast indicates that a parabola best describes the locus effect (Steel and Torrie 1980). For all analyses, we used the statistical-software package Genstat (Version 5.4.1; Anonymous 1993).

RESULTS

Feather replacement for the 15-yr period is portrayed in Table 1. In 1984, tail molt for this adult was complete (i.e., 12 feathers replaced). Although many species of small raptors go through a complete, annual, tail molt, the maximum number of rectrices Bloom and Clark (2001) observed replaced in wild eagles in 1 yr was nine. This unusual 1984 tail molt may have been due to the change in diet or latitude and was likely due to the heavily-worn nature of the tail (suggesting that eagles have a physiological or behavioral mechanism to detect wear and remove heavily worn feathers). The female did not lay eggs in 1984, and breeding has long been recognized to disrupt, postpone, and otherwise interfere with molt (Ginn and Melville 1983), so this may have been a factor.

The stress of the move to Arizona or being tethered for the first winter may also have been involved (physiological stress as been associated with excessive molt in non-eagles; Payne 1972). After 1984, the eagle never lost more than eight feathers in one molt season (Table 1).

After the eagle replaced all 12 rectrices in one season, 3 yr were required before the eagle was routinely replacing ca. half of its rectrices each year (Table 1). For wild eagles, the number of rectrices dropped in one season ranged from 1–9 (Bloom and Clark 2001). Feathers at some loci were replaced more often than others (Table 1). The L and R central feathers (loci 1) and the outermost feathers or laterals (loci 6) were replaced most often (Fig. 1), whereas the feathers at loci 2–4 were retained longest (>2 yr).

A mean of 6.0 feathers were lost per year for the 15 molting seasons monitored (Table 1). If we exclude the three extreme years (1984–86; 12, 2, and 8 feathers), the mean was similar (5.7 feathers/yr; 1987–98). Overall the mean retention time of individual rectrices (Fig. 1) was 24.4 mo and ranged from 12–36 mo ($N = 63$).

The effect of locus (Table 2) was statistically significant ($F_{5,51} = 4.48$, $P = 0.002$) due to differences in retention times for feathers at different feather positions as indicated by the highly significant quadratic contrast of locus ($F_{1,51} = 18.99$, $P < 0.001$). Deviations from this parabolic shape of the locus effects were not significant ($F_{3,51} = 1.03$, $P = 0.388$).

Rectrix-retention time was symmetric (i.e., there was no significant effect of side), and the interactions between side and locus contrasts were nonsignificant (Table 2), so we pooled data for matched loci L and R and obtained the following least squares averages: 22.0 (± 1.2)



Figure 1. Tail showing mean retention times in months (arithmetic means [minimum and maximum retention times]) at all 12 feather loci. Feathers were digitally altered to reflect mean times. Lightened feathers were replaced more frequently, very dark feathers least frequently. Rectrices are numbered from the center (R1, L1) to R6 at lower left and L6 at lower right.

mo at loci 1; 26.3 (± 1.3) at 2; 26.3 (± 1.4) at 3; 28.5 (± 1.4) at 4; 23.9 (± 1.2) at 5; and 21.8 (± 1.2) at loci 6.

Rectrix molt usually extended from late May (8 of 13 yr) until early August (tail molt ended between the end of July and late August in 10 of 13 yr). At the earliest, the first rectrix fell in mid May; the latest date that the first rectrix fell was in late July. The earliest date of the last rectrix falling was in early July; the latest was early September.

DISCUSSION

The primary function of molt is the replacement of damaged feathers. Feather damage is known or believed to derive from abrasion, mechanical stress during flight, bleaching, fungal and bacterial decomposition, and ectoparasites (Burt 1979, Burt and Ichida 1999, Ginn and Melville 1983, Serra 2001). More heavily pigmented feathers are generally believed to wear better (Voitkevich 1966, Serra 2001). A bird could theoretically strengthen

Table 2. Effects of side and rectrix position (locus) on feather retention time in a female Golden Eagle from 1984–98. The effect of locus and its interactions with side were partitioned into orthogonal polynomial contrasts to test our hypothesis that mid-span feathers on each side (loci 3, 4) are retained longer than are central and marginal feathers (loci 1, 5, and 6).

SOURCE OF VARIATION	df	SS	F	P
Side	1	2.50	0.15	0.698
Locus	5	368.43	4.48	0.002
Linear contrast	1	5.68	0.35	0.559
Quadratic contrast	1	312.02	18.99	<0.001
Deviations	3	50.73	1.03	0.388
Side \times locus	5	58.50	0.71	0.617
Side \times locus (linear)	1	18.72	1.14	0.291
Side \times locus (quadratic)	1	32.04	1.95	0.169
Side \times locus (deviations)	3	7.81	0.16	0.924
Residual	51	838.05		
Total	62	1267.56		



Figure 2. Juvenal rectrices at high-wear and low-wear loci from a second year Golden Eagle after ca. 15 mo of wear. The left-central rectrix (L1, left most feather) shows the greatest breakage and fraying and is shattered on both webs. Moving right (loci L2, L4, and L6 are illustrated), feathers show decreasing wear, and such wear is primarily on the outer (solar-exposed) web. Bird found shot near Flagstaff, AZ, 19 October 2000.

its tail or extend the “life” of its feathers by increasing pigmentation and it could, through natural selection, alter the size, shape, or number of feathers in high-wear/high-stress loci. Another means of compensating for differential wear is to replace feathers at high wear loci more frequently.

The need for different molt rates at various loci is demonstrated by wear patterns in wild eagles. Four feathers, all having been in the tail for the same amount of time, wore at vastly different rates (Fig. 2). The central feathers showed greatest wear and laterals the least. Thus, it is clearly adaptive to replace the most heavily worn central feathers more frequently. It is less easy to explain why the

lateral rectrices were also replaced more frequently in our captive adult (Fig. 1). Bloom and Clark (2001) found that wild yearlings normally replaced rectrices at loci 1 first, then at 6. From the inspection of the tails of museum specimens, direct trauma to the feathers (presumably incurred mostly while capturing prey) may also be somewhat more prevalent at loci 6 than at loci 3–5. However, we feel that a better explanation for the high-replacement rate for lateral feathers derives from their aerodynamic importance in minimizing turbulence, and therefore drag, as the tail cuts through the air stream (Thomas 1993).

We recorded 11 instances of rectrices being retained

longer than 2 yr (Table 1). None of these feathers were at loci 1 or 6. Nine of the 11 were adjacent to growing feathers. Based on these observations we suggest the existence of a physiological mechanism to avoid simultaneously replacing adjacent feathers, a hypothesis consistent with Servheen's (1976) observations. It seems likely that large gaps in the tail are maladaptive by causing aerodynamic instability (Thomas 1993) and by weakening the tail so that growing or unsupported feathers are more likely to be damaged.

For the two other feathers retained longer than 2 yr, two factors may help explain this retention. First, both feathers had grown in late in the season (i.e., their predecessors were molted around 1 August), so a delay in molting 2 yr later resulted in a postponement of molt until the next (third) season. Also, both were at loci where prolonged retention was normal (loci R4, 1993; and L3, 1995; Table 1).

In our captive adult, feathers skipped in one molt were normally (10 of 11 times) replaced early in the following molt. Five (of the 11) were the first rectrices dropped the following season, and one more was lost within a few days of the first rectrix being dropped.

From short-term observations of tail molt in three Golden Eagles, Servheen (1976) concluded that central feathers always molt at least 35 d apart and R1 always precedes L1. For our study eagle, in 1 yr (1988) when both central feathers molted, R1 dropped less than a mo before L1. From our molt data for two other captive Golden Eagles (the Kluane Lake and Montana eagles), left centrals twice fell before the right, so both of Servheen's observations have exceptions.

In conclusion, the general molt pattern is to replace alternate feathers in any one season. Normally, feathers were retained at least 2 yr, with protected feathers (loci 2–4) retained ca. 30% longer. The most consistent circumstance associated with the failure of a feather to molt after two seasons was the presence of a growing feather in an adjacent follicle. Feathers in high-wear positions (loci 1 and 6) consistently molted in alternate years, occasionally more often. This trend is left-right symmetrical. For our well-fed experimental bird, if a feather was retained in the second molt season after replacement, it was nearly always replaced in the first rectrix "molt wave" the following year. The physiological mechanisms controlling these phenomena are at present, unknown. We emphasize that this study was primarily based on data collected from one well-fed captive eagle. How well the patterns described here reflect molt in wild birds that experience periods of food stress and continually stress rectrices during flight and daily hunting activities is unknown. Nor do we know of the prevalence of this mechanism in other species for which the annual tail molt is incomplete.

RESUMEN.—La muda de la cola fue registrada duramente un periodo de 15 años en cautiverio de un águila dorada

(*Aquila chrysaetos*). En promedio solo seis (de 12) rectrices en posiciones mas desgastantes (ejemplo centrales y laterales) fueron remplazadas mas frecuentemente. Las plumas centrales mostraron los niveles mas altos de degradación solar. Las rectrices externas las cuales soportan más estrés y son de importancia aerodinámica en el margen de la cola, también fueron remplazadas más frecuentemente. Las plumas en posiciones protegidas fueron retenidas un 30% mas tiempo que las rectrices centrales o laterales. Estas observaciones conllevaron a la hipótesis que la muda de rectrices tiene una característica adaptativa en la cual se reemplazan más frecuentemente que las plumas de posiciones de alta importancia. El mecanismo de control de esta muda diferencial es desconocido
[Traducción de César Márquez]

ACKNOWLEDGMENTS

Our thanks go to Greg Depner and Joel Scrafford (Fish and Wildlife Service special agent) for handling transfer of the eagle to D. Ellis. Tom and Linda Averill, formerly co-owners of the Red Lodge Zoo made the eagle available for the study, gratis. The manuscript benefited from reviews by S. James Reynolds, Ann E. Edwards, Michael Kochert, and Peter Bloom. Our thanks to the late Walter and Sally Spofford for sharing molt data on one eagle. M. Kéry was supported by a grant (81ZH-64044) from the Swiss National Science Foundation.

LITERATURE CITED

- ANONYMOUS. 1993. Genstat 5: reference manual. Clarendon Press, Oxford, U.K.
- BLOOM, P.H. AND W.S. CLARK. 2001. Molt and sequence of plumages of Golden Eagles and a technique for in-hand ageing. *N. Am. Bird Bander* 26:97–116.
- BURTT, E.H., JR. 1979. Tips on wings and other things Pages 75–110 in E.H. Burtt, Jr. [ED.], *The behavioral significance of color*. Garland STPM Press, New York, NY U.S.A.
- AND J.M. ICHIDA. 1999. Occurrence of feather-degrading bacilli in the plumage of birds. *Auk* 116:364–372.
- ELLIS, D.H. 1979. Development of behavior in the Golden Eagle. *Wildl. Monogr.* 70.
- GINN, H.B. AND D.S. MELVILLE. 1983. Molt in birds. BTO Guide 19. British Trust for Ornithology, Hertfordshire, U.K.
- GRUBB, T.C., JR. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. *Auk* 106:314–320.
- JOLLIE, M. 1947. Plumage changes in the Golden Eagle. *Auk* 64:549–576.
- PAYNE, R.B. 1972. Mechanisms and control of molt. Pages 103–155 in D.S. Farner and J.R. King [EDS.], *Avian biology*. Vol. 2. Academic Press, New York, NY U.S.A.
- SERRA, L. 2001. Duration of primary molt affects primary quality in Grey Plovers *Pluvialis squatarola*. *J. Avian Biol.* 32:377–380.

- SERVHEEN, C. 1976. Deck-feather molt in Bald and Golden eagles in relation to feather mounting of radio transmitters. *Raptor Res.* 10:58–60.
- STEEL, R.G.D. AND J.H. TORRIE. 1980. Principles and procedures of statistics, 2nd Ed. McGraw-Hill, Auckland, New Zealand.
- SUSHKIN, P.P. 1900. Taxonomic notes on *Aquila*. *Bull. Br. Ornithol. Club* 11:6–10.
- THOMAS, A.L.R. 1993. The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners. *Proc. R. Soc. Lond.* 254:181–189.
- TJERNBERG, M. 1977. Individuell igenkänning av kungsnar *Aquila chrysaetos* i fält samt resultat av vinterinventeringar i sydvästra uppland. *Vår Fågelvärld* 36:21–32.
- VOITKEVICH, A.A. 1966. The feathers and plumage of birds. Sidgwick and Jackson, London, U.K.
- WATSON, J. 1997. The Golden Eagle. T. & A.D. Poyser, London, U.K.

Received 9 July 2003; accepted 14 March 2004

J. Raptor Res. 38(3):275–277

© 2004 The Raptor Research Foundation, Inc.

A LOCAL CONCENTRATION OF SNOWY OWLS ON THE YUKON-KUSKOKWIM DELTA IN SUMMER 2000

CHRISTOPHER M. HARWOOD,¹ BRIAN J. MCCAFFERY, FRED J. BROERMAN, AND PAUL A. LIEBERG²
U.S. Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, P.O. Box 346, Bethel, AK 99559 U.S.A.

KEY WORDS: *Snowy Owl*; *Bubo scandiacus*; *Yukon-Kuskokwim Delta*; *Yukon Delta National Wildlife Refuge*, *Alaska*.

we describe the magnitude of this unusual local summer concentration.

Snowy Owls (*Bubo scandiacus*) are nomadic and irregular summer visitors in Alaska (Gabrielson and Lincoln 1959, Parmalee 1992), particularly south of their stronghold on the northern arctic-coastal plain (e.g., Barrow). Near Hooper Bay on the Yukon-Kuskokwim Delta (YKD) in southwestern Alaska, Snowy Owls nested commonly (ca. 40 nests) in 1924 (Murie 1929). Despite the extensive activities of biologists in the decades following (particularly since the 1970s), concentrations comparable to those in 1924 have never been reported, and breeding records are virtually nonexistent. The only subsequent report of large numbers of Snowy Owls on the YKD was in 1963, when perhaps as many as several dozen (some nesting) were detected at the eastern end of Nelson Island (Nyctea Hills; J. King pers. comm.).

In summer 2000, Yukon Delta National Wildlife Refuge (YDNWR) personnel flew a series of aerial surveys to document distribution and abundance of fall-staging Bristle-thighed Curlews (*Numenius tahitiensis*). During these surveys, Snowy Owls were recorded regularly. In this paper,

STUDY AREA

The study area was located on the coastal YKD south of Nelson Island (Fig. 1). The roughly triangular area was bounded on the north by the 60°30' parallel, on the southwest by the Bering Sea, on the southeast by the Kinak River, and on the east by Dall Lake (Fig. 1). Elevations ranged from sea level to 135 m above sea level (masl) at the summit of Tern Mountain; however, more than 90% of the study area was <10 masl. This 2545-km² area included four major vegetation associations dominated by a variety of subarctic tundra types. North of Tern Mountain, a 5-km wide band of low wet graminoid meadows was immediately adjacent to the shoreline. Inland of these coastal meadows, there was a wide band of slightly higher tundra, varying in width from 5–30 km. This habitat was characterized by a series of low, ancient beach ridges, a high density of medium-sized lakes, and a slightly more heterogeneous mosaic of plant communities. Although graminoid meadows still dominated, more mesic communities, including graminoid tussock dwarf shrub peatland and lichen dwarf shrub peatland occurred here. Together, these two major habitats comprised the coastal zone of the study area. Farther inland, particularly east of Kegum Kagati Lake, and extending to Dall Lake (Fig. 1), large lakes were prevalent, and the three previously described plant communities were more evenly distributed. Finally, six scattered uplands comprised the only vegetation association in the study area >10 masl. Five of these exceeded 30 masl, and all five supported communities of dwarf shrub heath. These latter two habitats comprised the inland/upland zone of the study area.

¹ Present address: U.S. Fish and Wildlife Service, Kanuti National Wildlife Refuge, 101 12th Ave. Room 262, Fairbanks, AK 99701 U.S.A.; e-mail address: christopher.harwood@fws.gov

² Present address: U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge, P.O. Box 270, Dillingham, AK 99576 U.S.A.

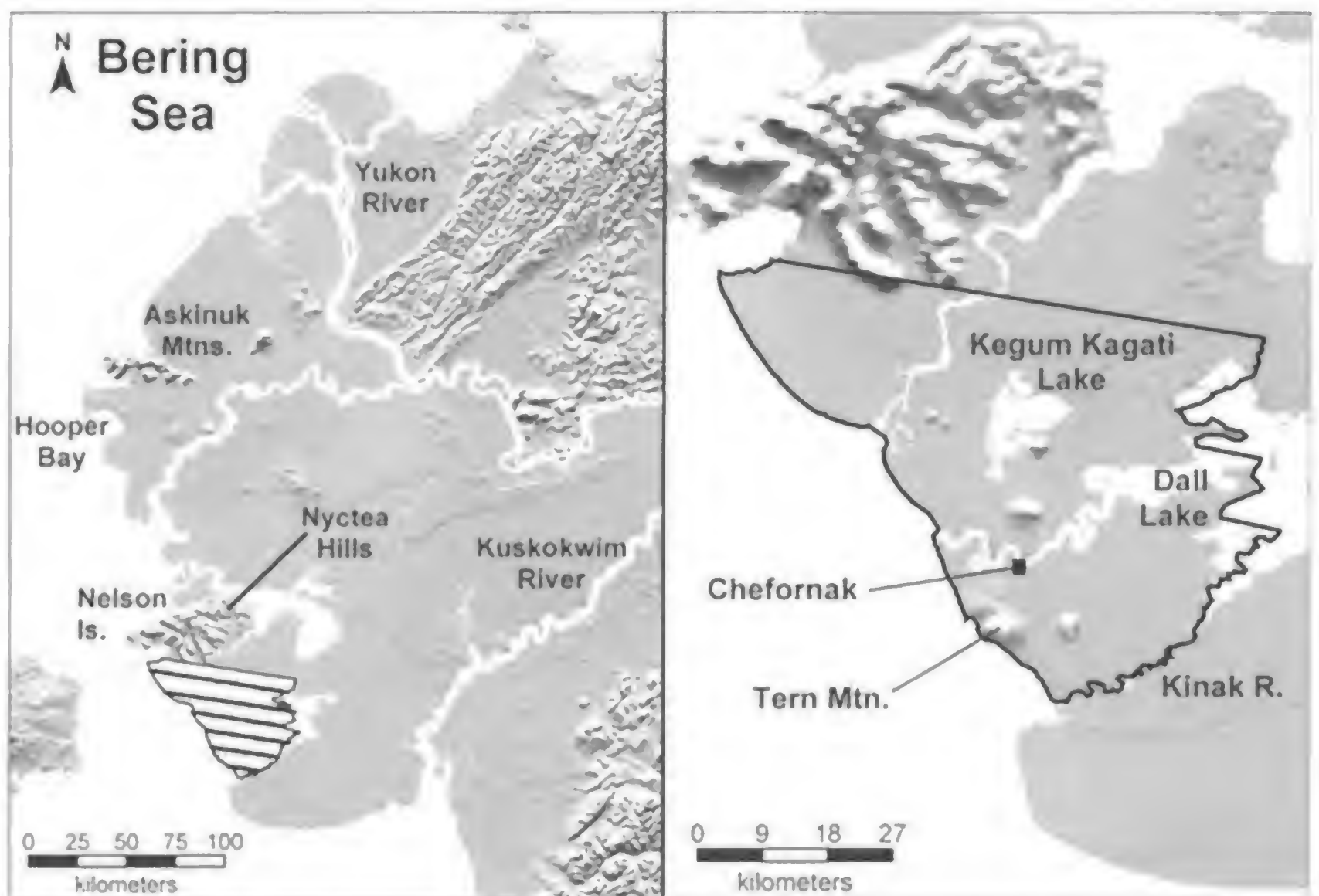


Figure 1. Yukon-Kuskokwim Delta in southwest Alaska (left panel; Snowy Owl survey area hatched) and detail of Snowy Owl survey area (right panel), summer 2000.

The coastal and inland/upland zones included 36% and 64% of the study area, respectively.

METHODS

We established 34 parallel transects of unequal length spaced 1.6 km apart in the study area in an east-west orientation. Five aerial surveys, spaced 2 wk apart, were conducted between 10 July and 14 September 2000. Surveys were flown in an Aviat Husky A-1B (on floats) at ca. 50 m above ground level and at ca. 90 kt. All 34 transects (total length = 1618 km) were flown in survey periods 1, 2, and 5, while only the 17 even-numbered transects (total length = 779 km) were flown for surveys 3 and 4. On each survey the rear-seat observer scanned a 300-m swath adjacent to the north-facing side of the aircraft (estimated by tape marked on the wing struts). Owl detections were recorded either into a tape recorder (along with time elapsed to calculate position) or Global Positioning System receiver. Owl detections were categorized as either "on transect" (i.e., within 300 m north of the aircraft) or "off transect" (i.e., all other observations, including those by pilot). Abundance estimates (and 95% confidence intervals) were derived exclusively from "on-transect" detections for each period (Cochran 1963, Caughley 1977). Abundance estimates were based on the assumption that all owls were detected in the 300-m sam-

ple area north of the transect lines. Owls were aged as adult or hatch-year on the basis of plumage differences (König et al. 1999).

RESULTS

Total detections (on transects) of Snowy Owls during survey periods ranged from 15–27 individuals, with the highest estimated number of Snowy Owls in the study area in survey period 4 (Table 1). Owls were not evenly detected throughout the study area; densities were markedly higher in the southern half, particularly concentrated southeast of Chefornak. Owls were also more likely to be detected in the inland (rather than the coastal) portion of the study area (on-transect observations: $N = 105$, $\chi^2 = 10.86$, $df = 1$, $P = 0.001$; off-transect: $N = 28$, $\chi^2 = 4.91$, $df = 1$, $P = 0.028$). Hatch-year birds, including at least one apparently attended by an adult, were detected in the two latter surveys (i.e., four owls during survey 4, one during survey 5). At least two possible nest sites (i.e., 3–5-m diameter circles of likely molted feathers) were recorded, but we did not land the plane to confirm these nests.

Table 1. Population estimates and 95% Confidence Intervals (CI) of Snowy Owls south of Nelson Island, Yukon-Kuskokwim Delta, AK, summer 2000.

DATES	TOTAL LENGTH OF TRANSECTS (km)	ACTUAL NO. OF OWLS DETECTED	ESTIMATE \pm (95% CI)
10–12 July	1618	15	79 \pm 48
24–25 July	1618	25	131 \pm 59
7–8 August	779	17	185 \pm 86
21–22 August	779	21	229 \pm 143
11–14 September	1618	27	142 \pm 63

DISCUSSION

While small numbers of Snowy Owls are observed regularly on the YKD in the nonbreeding season, the numbers observed in summer 2000 represent the largest concentration reported on the Delta in almost 40 yr. Since at least 1984, regional arvicoline rodent population highs on the YKD have occurred on a 4-yr cycle. Higher breeding densities of rodent-eating raptors, including Rough-legged Hawks (*Buteo lagopus*) and Short-eared Owls (*Asio flammeus*), are frequently associated with these peaks in rodent numbers (YDNWR unpubl. data). The year 2000 was no exception, with arvicoline rodents again showing regional population highs. Locally high breeding densities of Rough-legged Hawks and Short-eared Owls were recorded north of our study area in the Askinuk Mountains and in the coastal lowlands of the central YKD, respectively (B. McCaffery and J. Morse unpubl. observations). However, Snowy Owls were absent from these areas (T. Bowman pers. comm.). We do not know what habitat or prey factors may have limited the Snowy Owl concentration to the area south of Nelson Island, nor do we know why owls were more abundant in the southern and inland portions of our study area.

While local nesting was not definitively confirmed, the detection of volant juveniles, as well as a couple of possible nest sites, suggests perhaps the southernmost mainland nesting for Snowy Owls in Alaska since 1973 (i.e., Goodnews and Chagvan bays; Petersen et al. 1991). Failure to detect juveniles until the final two surveys might be partly explained by the species' lengthy (ca. 50 d; Parmalee 1992) and cryptic brood-rearing period. Appearance of volant young on 21 August suggests laying in late May–early June, which is consistent with Brandt's (1943)

observations in 1924. In spite of the abundance of adults present in 2000, it is unlikely that the magnitude of breeding rivaled that observed at Hooper Bay in 1924 (Murie 1929).

RESUMEN.—La concentración de verano mas grande reportada de el buho nival (*Bubo scandiacus*) en 40 años en el delta del Yukon-Kuskokwim fue documentada al sur de la Isla Nelson en el 2000. Los estimativos de abundancia de cinco monitoreos aéreos oscilaron entre 79–229 individuos en una área de estudio de 2545 km² cuadrados. La presencia de varios búhos juveniles sugieren la reproducción en el área de estudio.

[Traducción de César Márquez]

ACKNOWLEDGMENTS

We thank the numerous researchers, pilots, and observers that have worked on the YKD for their observations and recollections, particularly T. Bowman, V. Byrd, B. Conant, C. Dau, R. Gill, D. Groves, J. King, C. Lensink, M. Lindberg, J. Morse, J. Sedinger, and M. Wege. J. Bednarz, D. Evans, and T. Swem reviewed the manuscript. R. Stehn provided valuable statistical assistance and C. Knight assisted with the figure.

LITERATURE CITED

- Brandt, H. 1943. Alaska bird trails. Bird Research Foundation, Cleveland, OH U.S.A.
- CAUGHLEY, G. 1977. Sampling in aerial survey. *J. Wildl. Manage.* 41:605–615.
- COCHRAN, W.G. 1963. Sampling techniques. 2nd Ed. John Wiley and Sons, New York, NY U.S.A.
- GABRIELSON, I.N. AND F.C. LINCOLN. 1959. Birds of Alaska Stackpole Co., Harrisburg, PA, and Wildl. Manage. Inst., Washington, DC U.S.A.
- KÖNIG, C., F. WIECK, AND J.-H. BECKING. 1999. Owls: a guide to the owls of the world. Yale University Press, New Haven, CT U.S.A.
- MURIE, O.J. 1929. Nesting of the Snowy Owl. *Condor* 31: 3–12.
- PARMALEE, D. 1992. Snowy Owl (*Bubo scandiacus*). In A. Poole, P. Stettenheim, and F. Gill [Eds.], The birds of North America, No. 10. The Birds of North America, Inc., Philadelphia, PA U.S.A.
- PETERSEN, M., D.N. WEIR, AND M.H. DICK. 1991. Birds of the Kilbuck and Ahklun Mountain regions, Alaska. *N. Am. Fauna* 76. USDI Fish Wildl. Serv., Ray Brook, NY U.S.A.

Received 23 September 2002; accepted 3 June 2004

PREMIGRATORY COMMUNAL ROOSTS OF THE LESSER KESTREL IN THE BOREAL SUMMER

PEDRO P. OLEA¹ AND RUBÉN VERA*Dpto. de Biología Molecular y Ciencias del Medio Ambiente, Faculty of Experimental Sciences, SEK University, Campus Santa Cruz la Real, Segovia E-40003 Spain*ÁNGEL DE FRUTOS² AND HUGO ROBLES*Dpto. de Biología Animal, Fac. de C.C. Biológicas y Ambientales, University of León, León E-24071 Spain***KEY WORDS:** *Lesser Kestrel*, *Falco naumanni*; *pre migratory aggregations*; *communal roosts*.

The Lesser Kestrel (*Falco naumanni*) is a small migratory falcon breeding in the Palearctic and wintering mainly in Africa (Siegfried and Skead 1971, Cramp and Simmons 1980). This species is considered to be a threatened species listed as Vulnerable (BirdLife International 2002). Although many aspects of their breeding biology have been studied (e.g., Negro et al. 1992, Donázar et al. 1993, Hiraldo et al. 1996, Tella et al. 1996a, 1996b, 1997) there is little known about the post-fledging period of this species (but see Bustamante and Negro 1994, García 2000, Olea 2001a). This period can be particularly critical for the survival of the juvenile falcons because recently fledged birds have little experience in foraging, and in avoiding predators and human activities (Anders et al. 1998). During the post-fledging period, Lesser Kestrels seem to increase significantly in their abundance in some areas in northern Spain, where breeding populations are small or nonexistent (e.g., Llamas et al. 1987, Jubete 1997, Román 1998, Olea 2001b) and gather in communal roosts (Olea 2001b, Ursúa and Tella 2001).

Avian communal roosting is thought to provide survival benefits (Blanco and Tella 1999) in terms of decreased predation risk and increased foraging efficiency (Beauchamp 1999). Some evidence also suggests that such roosts could facilitate social relationships with implications in the regulation and viability of bird populations (Blanco et al. 1993, Blanco and Tella 1999) and in the conservation of some raptor species (Donázar et al. 1996). To manage and conserve a bird population, it is necessary to understand the requirements and the limiting factors of a population throughout the annual period (Steenhoff et al. 1984). For Lesser Kestrels, information on summer communal roosts is incomplete. The species has been studied during winter in Spanish areas (Negro et al. 1991) as well as in Africa (austral summer; Siegfried and Skead 1971, Kopp 2002). To our knowledge, the only published information on Lesser Kestrel

roosts during the summer in the Palearctic comes from Spain and Italy, and consists of anecdotal records of two roosts (Tejero et al. 1982 and Aparicio 1990, respectively) and on the monitoring of birds at four roosts during a single summer (Palumbo 1997, Olea 2001b, Ursúa and Tella 2001). Here, we examine the use of communal roosts by Lesser Kestrels in northwestern Spain during three summers. We describe roost site characteristics and examine numbers and temporal variation of roosting Lesser Kestrels.

METHODS

Communal roosts were located in the province of León, northwestern Spain, at about 800 m above sea level, between the towns of Santa Marta and Sahagún (42°25'–42°17'N, and 5°23'–5°06'W; 11.7°C annual mean temperature and 486 mm rainfall). The study area covers 384 km² devoted to cereal crops. This area was selected because communal roosting was observed previously (Olea 2001b; pers. obs.). In 2002, we documented 23 breeding pairs of Lesser Kestrels in the study area. The landscape was flat and open, with practically no trees. The area is broken up by a number of small seasonal streams flowing in a north-south direction. When this study was conducted, the fields had been partially harvested and the area was mostly dominated by stubble and fallow fields (74% of the area). The area is also crossed by a recently-built highway.

Roost Site Detection. An effort was made to find all roosts in the study area. We looked for roost sites between 20–26 August 1998. In 2001 and 2002 the search for roosts began on 25 July and 1 July, respectively. We first checked the roosts used by Lesser Kestrel in previous years. Next, we searched for new roosts in the area until the end of the summer. Several observers with binoculars (8×) and telescope (20–60×) were distributed across the area at the best vantage points. Roosts were located during late afternoon, because during this period the Lesser Kestrels tended to gather around “staging” areas near roosts. These aggregations were fairly conspicuous and easy to detect. From these sites, kestrels progressively moved toward the roost sites about an hour before sunset.

Monitoring of Roosting Birds. We counted birds at the roosts between 26 August and 26 September in 1998 (every 3–7 d, 7 monitoring d), between 25 July and 10 Oc-

¹ E-mail address: pedro.olea@sekmail.com

Table 1. Characteristics of the premigratory communal roosts of Lesser Kestrels during summers of 1998, 2001, and 2002 in northwestern Spain. Study periods: 26 August–8 September 1998, 25 July–10 October 2001, and 1 July–9 October 2002.

SUBSTRATE	ROOSTS						
	A EVERGREEN OAK	B PYLONS (380 kV)	C BLACK LOCUSTS AND COMMON PEAR	D POPLAR PLANTATION	E SEVERAL UTILITY POLES (<45 kV)	F PYLON (380 kV)	G POPLAR PLANTATION
Distance to power-line (kV) in m	30 m (45 kv)	0 m (380 kV)	20 m (<45 kV)	40 m (380 kV)	0 (<45 kV)	0 (380 kV)	40 m (<45 kV)
Max. no. of kestrels							
1998	355 (29 August)	262 (31 August)	96 (2 September)	106 (8 September)			
2001	200 (12 August)			750 (31 August)	27 (31 August)	7 (6 September)	85 (18 September)
2002	360 (4 September)			641–666 (2 August)			

tober in 2001 (every 1–17 d, 14 monitoring d) and between 1 July and 9 October in 2002 (every 1–11 d, 23 monitoring d). In 1998 and 2001, we began to count birds at roosts on 26 August and 25 July, respectively, after the Lesser Kestrels began using roosts. For this reason, in 2002 we initiated monitoring several weeks before the previous years to determine accurately the date when Lesser Kestrels started to use the roosts.

Except in 1998, we tried to census Lesser Kestrels using all roosts simultaneously. Only one roost was monitored in 1998; in 2001 and 2002, the two largest and more-stable roosts were monitored during the entire study period. Observation sites were at ground level and 300–600 m away from the roosts. Individuals were counted using binoculars and 20–60 \times spotting scopes. To avoid bias in the counting between observers, the same persons monitored the same roosts. Although this does not eliminate potential biases among roosts, counts of Lesser Kestrels in the roosts were facilitated by their behavior. Specifically, before roosting, kestrels perched on powerlines, where time was spent preening, or bathed in the sand. Thus, we believe that the census of kestrels was reliable.

We counted individuals going to roosts in 2.5–5 min intervals from 30 min before sunset until all individuals entered the roost. The highest evening count was used as the roost count for that day. In roost A, we censused Lesser Kestrels when perching on powerlines close to the small and scattered group of evergreen oak trees (*Quercus ilex*), which they used as roost sites (Table 1). At this roost, birds flew as singles, in pairs, or in small groups from the wires to the trees, but not in the opposite direction. This made counting kestrels relatively easy.

In 2002, we could not obtain accurate counts of Lesser Kestrels entering one of the roosts on several occasions (6 of 23 censuses) because roosting activity was erratic. Therefore, kestrels were counted immediately following sunrise leaving the roost (from 30 min before sunrise until after all the kestrels left the roost).

RESULTS

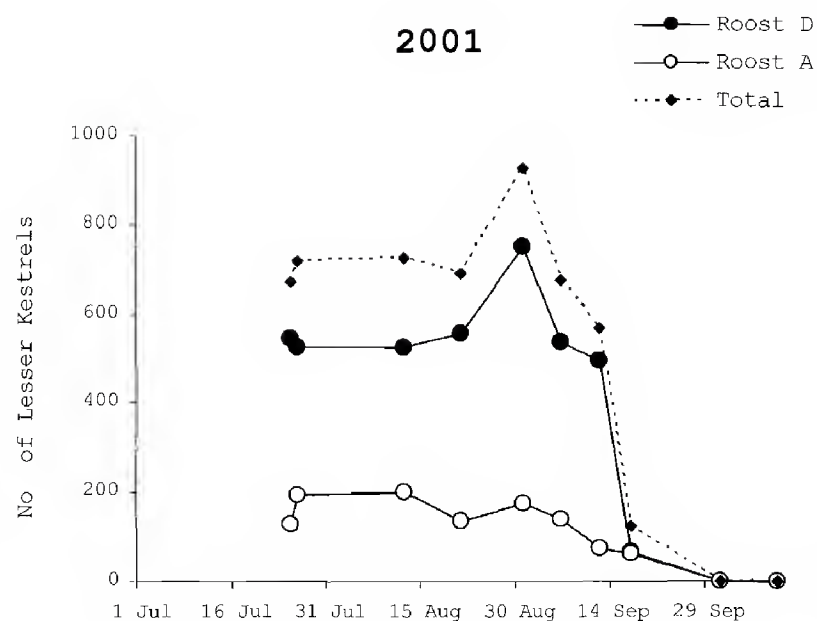
Description of the Roost Sites. In 1998, four communal roosts of Lesser Kestrels were found. Roost site A was located in a small evergreen oak forest, where Lesser Kestrels used a group of five scattered evergreen oaks 5–8 m high, and close to a road (<150 m; see Table 1). Roost B, was located on three utility pylons (380 kV). More than 90% of the individuals roosted on a single pylon. Roost C was on three trees (two black locusts [*Robinia pseudoacacia*] and common pear [*Pyrus communis*]) 6–7 m high. Roost D was in a poplar (*Populus* sp.) plantation of 612 m² with poplars 20–28 m high.

All four roosts were in the vicinity of powerlines (<50 m), ranging from <45 –380 kV (Table 1), where the birds grouped, rested and preened before going to the roost. The shortest distance between roost sites was 6 km (between roosts A and C), and the longest, 17 km (between roosts A and D).

In 2001, we located four roosts, two of them were the same as in 1998 (A and D). The two new roosts were on electric poles (E on several <45 kV poles and F on 380 kV poles). In 2002, Lesser Kestrels used roosts A and D, but in roost A the birds used a larger number of evergreen oaks in the forest than in 1998 (see above).

Change of Roost Sites within the Year. On 10–12 September 1998 some changes in the roost sites were observed: kestrels stopped using roost B and roost A was moved 0.5–1.5 km from the previous roost location. On 17–18 September 2001, the kestrels in roost D split into three groups, one stayed in roost D, another moved to roost G, and the third group of kestrels left and were not located. In 2002, the kestrels in roost D split temporally (between 27 and 29 August) in three groups, using two other nearby plantations of poplars (not included in Ta-

1a



1b

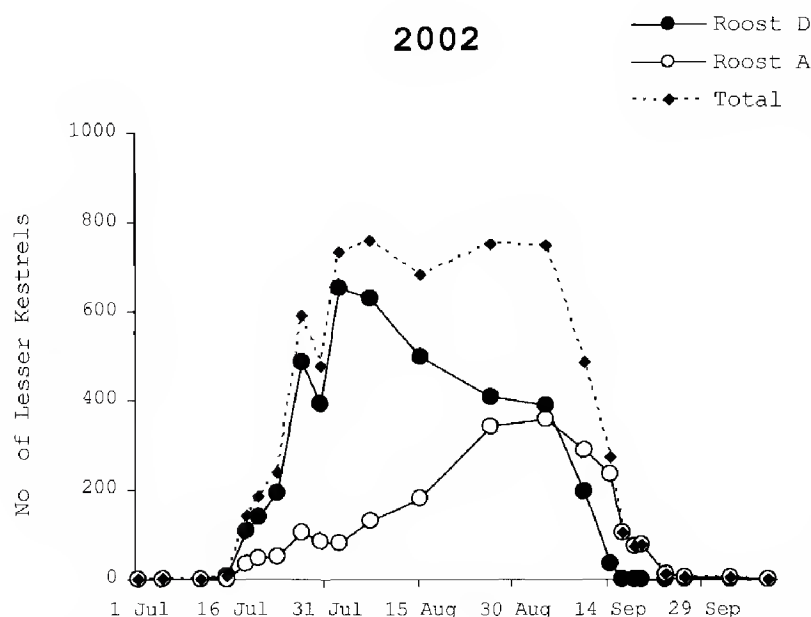


Figure 1. Seasonal variation of Lesser Kestrel abundance at roosts A and D, and total number (sum of kestrels using main roosts A and D); in summer of 2001 (a), and summer of 2002 (b).

ble 1). Later that year (between 29 August and 4 September), roost D was reused.

Roost Dynamics. In 1998, the mean number of Lesser Kestrels in roost A was 320 until 10 September; this number peaked on 29 August, with 355 individuals. The number of Lesser Kestrels decreased markedly after 10 September (particularly between 10–17 September), until 26 September, when no individuals were detected at the roost.

The abundance pattern of roosting Lesser Kestrels at roosts A and D varied between 2001 and 2002. During 2001, the number of birds in roost D tended to be about three times higher than in roost A (Fig. 1a). The maximum number of birds in roost D was 750 (31 August),

and 200 birds in roost A (12 August). The number of Lesser Kestrels decreased markedly after 7 September in both roosts. From October, no birds were observed in the roosts. The maximum number of birds summing up both roosts, simultaneously censused, was 925 (31 August; Fig. 1a). Two other small roosts (E and F) were used in 2001 (Table 1).

In 2002, the first birds using the roosts were observed on 15 July and 18 July in roosts D and A, respectively (Fig. 1b). Use of the two roosts by kestrels through time during the post-fledgling period differed in 2002. Roost D increased markedly until 2 August (peak = 653 birds), while kestrels at roost A steadily increased until 4 September with 360 birds (Fig. 1b). No birds were observed in roost D on 16 September, while there were no birds in roost A on 3 October. The maximum number of birds, summing up both roosts, was 761 in 2002 (7 August; Fig. 1b).

Roosting Behavior. During 2001 and 2002, the roosting behavior was different at the two primary roosts observed (D and A). At roost D, the birds formed generally a cloud-like flock circling above the roost ca. 10 min before entering the roost. However, at roost A the birds flew directly from powerlines or the ground to roost as singles, in pairs, or in small groups. Lesser Kestrels entered the roosts from sunset until ca. 30 min later. In 2001, Lesser Kestrels entered the roosts between 3 and 34 min after sunset. In 2002, Lesser Kestrels entered the roosts from 1.3 min before–23 min after sunset.

DISCUSSION

In the study area, close to 1000 Lesser Kestrels used communal roosts at some point during the summer. Similar aggregations have been found during this period in northeastern Spain (Ursúa and Tella 2001). Because our study area had only 23 Lesser Kestrel breeding pairs in 2002, the large population we found using roosts in summer indicates that most birds were adults or juveniles coming from other areas, as previously suggested by other authors (García 2000, Ursúa and Tella 2001) and supported with observations on post-fledgling dispersal (Olea 2001a).

In our study area, Lesser Kestrel used the roosts from mid-July until late September. This temporal pattern differs somewhat from that found by Ursúa and Tella (2001) in two roosts in northeastern Spain (Navarra), where birds used the roosts from early June. This difference could be due to the fact that the Navarra roosts could be used by the local population during the breeding period, contrary to what has been observed in our study area. Another possible explanation would be that there are differences in breeding phenology and/or variations in the dates of first occupancy of roosts among years.

The number of birds at the roosts increased from mid-July, probably due to the arrival of post-breeding individuals. The decrease in the number of Lesser Kestrels from September coincided with the migration to winter quar-

ters (Bernis 1980), and was consistent with observations by Ursúa and Tella (2001). The maximum of birds, summing up the two larger roosts simultaneously censused, was reached in August in both years (Fig. 1). This agrees with what has been observed in Navarra (Ursúa and Tella 2001) and Italy (Palumbo 1997). Nevertheless, the date of the maximum number of birds varied between roosts, especially in 2002 (Fig. 1b). The cause of this difference between the roosts A and D is not clear, but it could be due to the fact that roost D was censused at sunrise during 6 d (between 27 July and 15 August; Fig. 1b). Kópić (2002) found Lesser Kestrels arriving to the roosts several hours after sunset, therefore the number of birds counted at sunrise may be larger than at sunset. If so, the peak observed on 2 August could be due to differences in the counting procedures. However, we do not know whether Lesser Kestrels arrived after sunset counts at the roosts we studied, and if that was so, what fraction of the population it represented. On the other hand, the observed negative trend in number of birds from 7 August (counted at sunrise) was maintained, although the censuses from 15 August were carried out at sunset, suggesting that such potential bias was minimal (Fig. 1b). Alternatively, the different dynamics of roosts A and D in 2002 could be due to interchange of individuals between roosts (individuals at roost D switched to using roost A later during the post-fledging period; Fig. 1b).

Lesser Kestrels returned to the study area year after year and were faithful in their use of communal roosts, with two roosts used at least during 3 yr, suggesting that this area could be used as a regular premigratory area. Areas occupied by a relatively high post-breeding population of Lesser Kestrel, such as our study area where the post-breeding numbers largely exceeds the breeding population, has also been found in northern Spain (Ursúa and Tella 2001), and this could be the case elsewhere (e.g., Jubete 1997, Román 1998). The apparent fidelity to roost sites suggests an important role for these summer areas. Aparicio (1990) and Morton (1992) have suggested that food supply is important during the period prior to migration when individuals molt and fatten, and may be a critical factor for the survival of some raptor species during dispersal (Newton 1979, Korpimäki and Lagerström 1988, Miller et al. 1997). Therefore, the availability of areas with sufficient food supply during this period (e.g., with high densities of Orthoptera, the main food of Lesser Kestrel; Franco and Andrada 1977, Tejero 1982; pers. obs.) could be important. In our study area high densities of grasshoppers occur primarily during summer, and this resource is used by the post-breeding Lesser Kestrel population (P. Olea and A. de Frutos unpubl. data), suggesting a role for this area as a premigratory feeding and staging area.

The ca. 1000 Lesser Kestrels counted in our roosts and the ca. 3000 birds found by Ursúa and Tella (2001) in two roosts in northern Spain, may indicate that a significant fraction of the Spanish Lesser Kestrel population

(12 000 breeding pairs; BirdLife 2002) gathered in only four roost sites in this post-fledging period, suggesting the importance of these sites for conservation (Ursúa and Tella 2001). Therefore, we suggest that further studies are required to identify other areas and roosts used by the Lesser Kestrel during the post-fledging period. Also, the potential role that these areas could be playing in the ecology and conservation of Lesser Kestrel populations needs to be examined.

RESUMEN.—Existe poca información sobre dormideros comunales estivales de cernícalo primilla (*Falco naumanni*) en la región Paleártica. Estudiamos los dormideros comunales de cernícalo primilla durante los veranos de 1998, 2001, y 2002 en un área agrícola (384 km² con 23 parejas reproductoras) en el noroeste de España. Los dormideros se buscaron intensivamente cada año por todo el área de estudio y se registró el número de cernícalos primillas que usaron los dormideros. Los dormideros se ubicaron en diferentes substratos, tanto naturales (árboles) como artificiales (torres de alta y baja tensión). Se localizaron cuatro dormideros de cernícalo primilla en 1998 (96–355 aves), cinco en 2001 (7–750 aves) y cuatro en 2002 (360–666 aves). Los dos dormideros con mayor número de cernícalos primillas fueron usados durante los tres años de estudio. El número máximo de cernícalos primilla en los dos dormideros más grandes fue de 925 aves en 2001 y 761 en 2002. El número de cernícalos primillas alcanzó el máximo en Agosto, probablemente por la llegada de individuos de otras áreas, y descendió en Septiembre, coincidiendo con la migración. La gran concentración de cernícalos y la fidelidad a los lugares usados como dormideros sugiere un importante papel de estas áreas en la ecología y conservación del cernícalo primilla.

[Traducción de los autores]

ACKNOWLEDGMENTS

We are grateful to Jesús Fernández, Rafael González, Olga Mora, Cristina Trigal, María del Carmen Cordero, Soledad, Irene Marcos, Rodolfo Pozuelo, Tania Velasco, Enrique Osorio, and Francisco J. Purroy for their help during the fieldwork. We thank Alvaro de La Puente, Jesús Fernández, and Rafael González, who loaned us their telescopes. Vittorio Baglione and two anonymous referees provided valuable suggestions on the manuscript. Juan José Prat improved the English. This research was partially supported by Monteleón-Caja España Foundation. A. de Frutos was financed by a predoctoral fellowship from the University of León.

LITERATURE CITED

- APARICIO, J.M. 1990. Actividad, selección del método de caza y balance energético diario de *Falco naumanni* durante el periodo premigratorio. *Ardeola* 37:163–178.
- ANDERS, A.D., J. FAABORG, AND F.R. THOMPSON. 1998. Post-fledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *Auk* 115:349–358.

- BEAUCHAMP, G. 1999. The evolution of communal roosting in birds: origin and secondary losses. *Behav. Ecol.* 10:675–687.
- BLANCO, G., J.A. FARGALLO, AND J. CUEVAS. 1993. Seasonal variations in numbers and levels of activity in a communal roost of choughs *Pyrrhocorax pyrrhocorax* in central Spain. *Avocetta* 17:41–44.
- AND J.L. TELLA. 1999. Temporal, spatial, and social segregation of Red-billed Choughs between two types of communal roost: a role for mating and territory acquisition. *Anim. Behav.* 57:1219–1227.
- BERNIS, F. 1980. La migración de las aves en el Estrecho de Gibraltar. Vol. 2. Aves planeadoras. Cátedra de Zoología. Univ. Complutense, Madrid, Spain.
- BIRDLIFE INTERNATIONAL. 2002. España incumple el plan de acción del cernícalo primilla. *Garcilla* 109:33–35.
- BUSTAMANTE, J. AND J.J. NEGRO. 1994. The postfledging dependence period of the Lesser Kestrel (*Falco naumanni*) in southwestern Spain. *J. Raptor Res.* 28:158–163.
- CRAMP, S. AND K.E.L. SIMMONS. 1980. The birds of the western Palearctic. Vol. 2. Oxford University Press, Oxford, U.K.
- DONÁZAR, J.A., J.J. NEGRO, AND F. HIRALDO. 1993. Foraging habitat selection, land-use changes, and population decline in the Lesser Kestrel *Falco naumanni*. *J. Appl. Ecol.* 30:515–522.
- , O. CEBALLOS, AND J.L. TELLA. 1996. Communal roosts of Egyptian Vulture (*Neophron pernopterus*): dynamics and implications for the species conservation. Pages 189–201 in J. Muntaner and J. Mayol [EDS.], *Biología y conservación de las rapaces Mediterráneas*. Actas IV Congr. Biol. Cons., Palma de Mallorca, Spain.
- FRANCO, A. AND J.A. ANDRADA. 1977. Alimentación y selección de presa en *Falco naumanni*. *Ardeola* 23:137–187.
- GARCÍA, J. 2000. Dispersión premigratoria del cernícalo primilla *Falco naumanni* en España. *Ardeola* 47:197–202.
- HIRALDO, F., J.J. NEGRO, J.A. DONÁZAR, AND P. GAONA. 1996. A demographic model for a population of the endangered Lesser Kestrel in southern Spain. *J. Appl. Ecol.* 33:1085–1093.
- JUBETE, F. 1997. Atlas de las aves nidificantes de la provincia de Palencia. Asociación de Naturalistas Palentinos, Palencia, Spain.
- KOPIJ, G. 2002. Food of the Lesser Kestrels *Falco naumanni* in its winter quarters in South Africa. *J. Raptor Res.* 36:148–152.
- KORPIMÄKI, E. AND M. LAGERSTRÖM. 1988. Survival and natal dispersal of fledglings of Tengmalm's Owl in relation to fluctuating food conditions and hatching date. *J. Anim. Ecol.* 57:433–441.
- LLAMAS, O., A. LUCIO, AND F.J. PURROY. 1987. Comunidades de falconiformes en la llanura cerealista del SE de la provincia de León: I Cong. Int. Aves esteparias. Junta de Castilla y León, León, Spain.
- MILLER, G.S., R.J. SMALL, AND E.C. MESLOW. 1997. Habitat selection by Spotted Owls during natal dispersal in western Oregon. *J. Wildl. Manage.* 61:140–150.
- MORTON, M.L. 1992. Effects of sex and birth date on pre-migration biology, migration schedules, return rates and natal dispersal in the mountain White-crowned Sparrow. *Condor* 94:117–133.
- NEGRO, J.J., M. DE LA RIVA, AND J. BUSTAMANTE. 1991. Patterns of winter distribution and abundance of Lesser Kestrel (*Falco naumanni*) in Spain. *J. Raptor Res.* 25:30–35.
- , J.A. DONÁZAR, AND F. HIRALDO. 1992. Copulatory behaviour in a colony of Lesser Kestrels: sperm competition and mixed reproductive strategies. *Anim. Behav.* 43:921–930.
- NEWTON, I. 1979. Population ecology of raptors. T. & A.D. Poyser, London, U.K.
- OLEA, P.P. 2001a. Post-fledging dispersal in the endangered Lesser Kestrel *Falco naumanni*. *Bird Study* 48:110–115.
- . 2001b. Sobre la dispersión premigratoria del cernícalo primilla *Falco naumanni* en España. *Ardeola* 48:237–241.
- PALUMBO, G. 1997. Il Grillaio. Altrimedia Edizioni, Matera, Italy.
- ROMÁN, J. 1998. Cernícalo primilla noticiario ornitológico. *Ardeola* 45:121.
- SIEGFRIED, W.R. AND D.M. SKEAD. 1971. Status of the Lesser Kestrel in South Africa. *Ostrich* 42:1–4.
- STEENHOFF, K., M.N. KOCHERT, AND M.Q. MORITSCH. 1984. Dispersal and migration of southwestern Idaho raptors. *J. Field Ornithol.* 53:357–368.
- TEJERO, E., M. SOLER, I. CAMACHO, AND J.M. ÁVILA. 1982. Contribución al conocimiento del régimen alimenticio del cernícalo primilla (*Falco naumanni*). *Bol. Estac. Cent. Ecol.* 22:77–82.
- TELLA, J.L., M.G. FORERO, A. GAJÓN, F. HIRALDO, AND J.A. DONÁZAR. 1996a. Absence of blood parasitization effects on Lesser Kestrel fitness. *Auk* 113:253–256.
- , F. HIRALDO, J.A. DONÁZAR, AND J.J. NEGRO. 1996b. Costs and benefits of urban nesting in the Lesser Kestrel. Pages 53–60 in D.M. Bird, D. Varland, and J.J. Negro [EDS.], *Raptors in human landscape*. Academic Press, London, U.K.
- , M.G. FORERO, J.A. DONÁZAR, J.J. NEGRO, AND F. HIRALDO. 1997. Non-adaptive adoptions of nestlings in the colonial Lesser Kestrel: proximate causes and fitness consequences. *Behav. Ecol. Sociobiol.* 40:253–260.
- URSÚA, E. AND J.L. TELLA. 2001. Unusual large communal roosts of Lesser Kestrel in two electric substations of northern Spain: implications for the conservation of Spanish population. Page 188 in J. Bustamante, G. Crema, E. Casado, J. Seoane, C. Alonso, C. Rodríguez, M. de Lucas, and G. Janss [EDS.], *Estación Biológica de Doñana*. Raptor Research Foundation, Sevilla, Spain.

Received 15 July 2003; accepted 26 May 2004
Associate Editor: Juan José Negro

J. Raptor Res. 38(3):283–286

© 2004 The Raptor Research Foundation, Inc.

ANALYSIS OF THE AUTUMN MIGRATION OF JUVENILE HONEY-BUZZARDS (*PERNIS APIVORUS*) ACROSS THE CENTRAL MEDITERRANEAN

NICOLANTONIO AGOSTINI¹

Via Carlo Alberto n°4, 89046 Marina di Gioiosa Jonica (RC), Italy

CHARLES COLEIRO

St. Michael Flat 2, Paris Street, Zebbug, Malta

MICHELE PANUCCIO

Via Mario Fioretti n°18, 00152 Roma, Italy

KEY WORDS: *European Honey-buzzard*; *Pernis apivorus*; migration; orientation; water-crossing.

The existence of innate-migratory orientation in many birds is supported by those cases in which juveniles migrate to wintering areas independently of adult birds (Marks and Redmond 1994, Berthold 2001). The European Honey-buzzard (*Pernis apivorus*) is such a species. This buzzard is a long-distance migrant with birds breeding in Europe and wintering in west-central equatorial Africa (Cramp and Simmons 1980). During autumn migration in the central Mediterranean area, adults passing through central Italy tend to follow the peninsula, crossing the Straits of Messina (between southern continental Italy and Sicily), then deviate westward using the same migration route as in spring between western Sicily and Tunisia (Agostini et al. 2000). This pattern suggests true navigational abilities (Agostini and Logozzo 1995, 1997, Agostini et al. 2000). Only juveniles that occasionally migrate in flocks of adults seem to be able to learn this route by information transmission (Agostini et al. 1999). However, more commonly, juveniles of this species tend to migrate 2 wk later than adults, after the first 10 d of September (Kjellén 1992, Agostini and Logozzo 1995, Schmid 2000). Similar to adults, juveniles often fly in flocks (Agostini et al. 1999, 2002). Hundreds of juveniles migrate along the Calabrian Apennines (southern continental Italy; Agostini and Logozzo 1995, 1997, Agostini et al. 1999) and cross the sea at its widest point between Sicily and Libya via Malta (Agostini et al. 1999, 2002), moving in a southwestern direction (Agostini and Logozzo 1995, Agostini et al. 1999; Fig. 1). Along the western coast of central Italy, a similar passage was recorded at the Circeo promontory (Corbi et al. 1999, Agostini et al. 2002; Fig. 1). At this site, birds apparently cross the Tyrrhenian Sea moving toward the island of Ponza, located about 30 km south-southwest of the promontory (Fig. 1).

However, contemporaneous observations made at the Circeo promontory and Malta during the second half of September 2000, showed a correspondence between migratory pulses of buzzards suggesting that juveniles tend to follow the Italian peninsula deviating southeast during

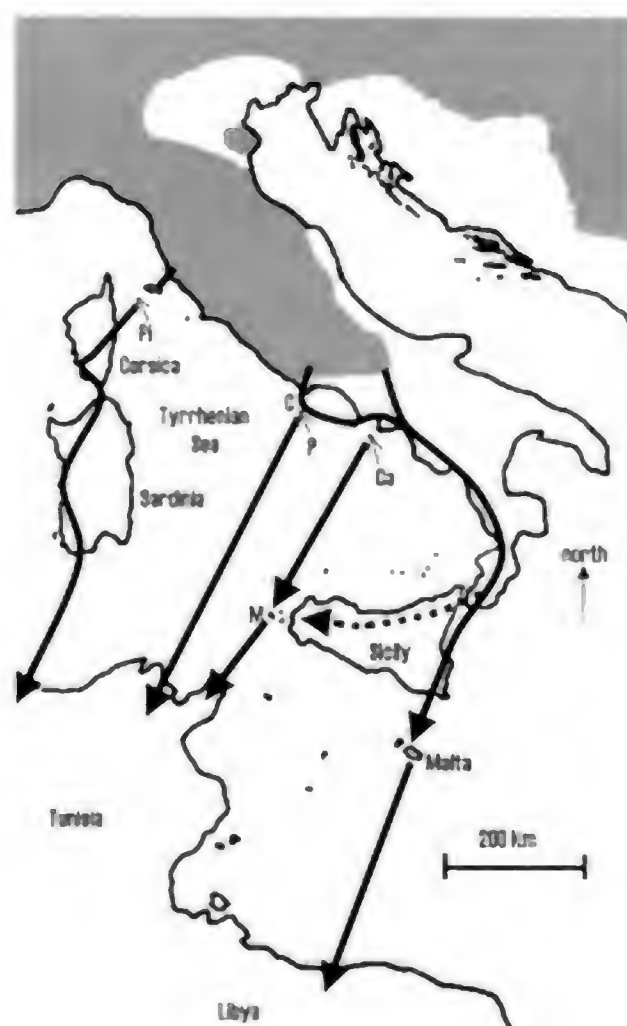


Figure 1. Study area and presumed routes used by juvenile European Honey-buzzards during the autumn migration across the central Mediterranean (Pi = Pianosa, C = Circeo, P = Ponza, Ca = Capri, M = Marettimo; dotted arrow: only migrating flocks of adults; the breeding areas of the honey-buzzard are shown in grey, [Gensbøl 1992]).

¹ E-mail address: nicolantonioa@tiscalinet.it

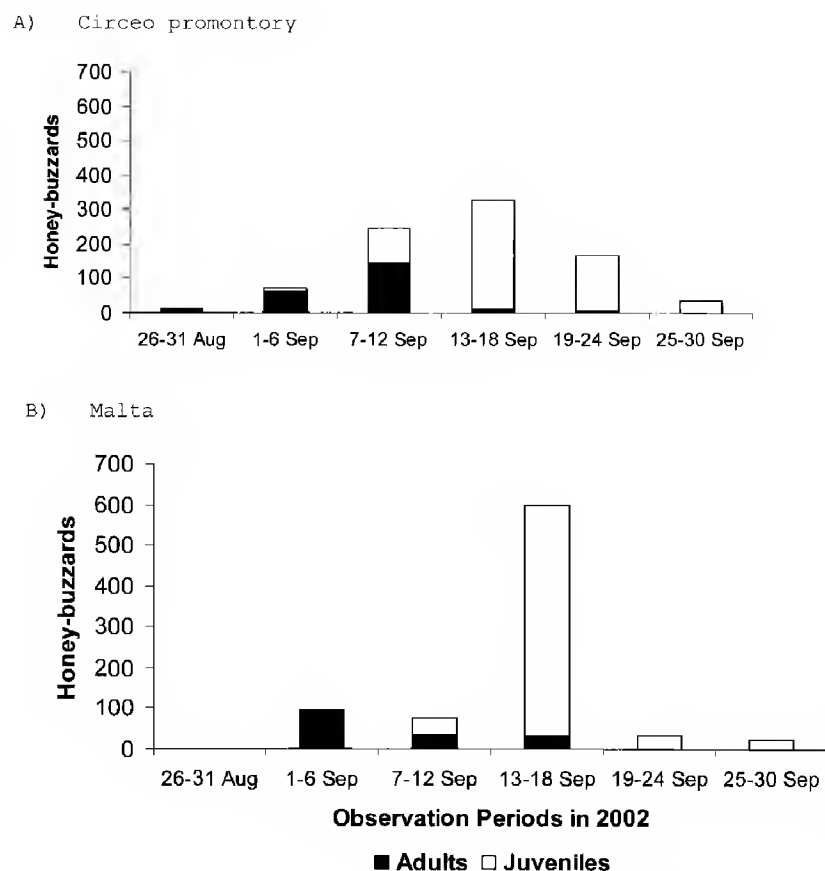


Figure 2. Adult and juvenile European Honey-buzzards estimated in the six 6-d periods at the Circeo promontory (A) and over Malta (B), according to their proportion among the identified individuals.

migration through central Italy (Agostini et al. 2002). Thus, juveniles may change their innate direction of migration (probably to the southwest), somewhat in response to geographic barriers (e.g., open water). The aim of this study was to test this suggestion by counting migrants at these two sites simultaneously during autumn 2002.

STUDY AREA AND METHODS

Observations were made between 26 August and 30 September 2002, each day from 0900 H until dusk aided with telescopes and binoculars. The Circeo promontory is located in the southernmost point of the Pianura Pontina reaching 541 m above sea level (masl; Fig. 1). At this location, we used an observation site (altitude ca. 400 m) in a military zone, on the roof of the Ente Nazionale Assistenza Volo building; from this look-out it was possible to observe birds undertaking a water-crossing toward the island of Ponza, which was nearly always visible. Malta is situated about 90 km south of Sicily and 335 km north of Libya (Fig. 1). Raptors concentrate along the cliffs on the western side of the island (Beaman and Galea 1974). The observation site was located in this area, on one of the highest points of the island (250 masl). We divided the 36 d of observation into six 6-d periods and attempted to distinguish adults and juveniles. Generally when buzzards were very close (<150 m) we were able to classify ages. The number of adults and juveniles was derived by multiplying their proportions in the sample of identified individuals to the total count during each 6-d period, following the method used in previous studies

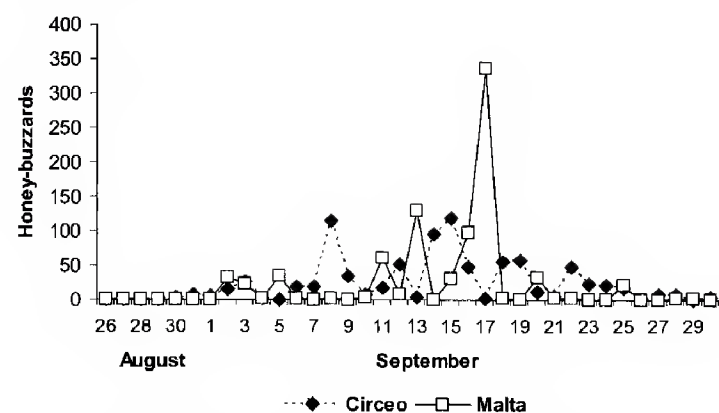


Figure 3. Occurrence of migrating European Honey-buzzards at Circeo and over Malta between 26 August and 30 September 2002.

(Agostini and Logozzo 1997, Agostini et al. 1999). Using direct visual sampling, we likely missed some proportion of migrants passing at both sites. However, our aim was to obtain a reasonable sample of birds to compare the variation of the migratory flows at the two study locations

RESULTS AND DISCUSSION

At the Circeo promontory, a total of 860 honey buzzards were counted; of these, 726 individuals undertook the crossing of the Tyrrhenian Sea toward the island of Ponza, 85 flew east-southeast along the coast while 49 birds roosted near the observation site. During the six 6-d periods, the passage of 235 (27%) adults and 625 (73%) juveniles was estimated (114 adults and 308 juveniles identified). Nearly all adults were seen during the first three 6-d periods (Fig. 2A). The daily variation of the migratory flow showed two pulses of movement on 8 and 14–16 September, when a total of 115 and 265 birds were counted, respectively (Fig. 3). Both adults and juveniles showed a strong tendency to remain in flocks after reaching the water barrier. Only on 10 occasions (7.8% of flocks, $N = 129$) did we observe individuals to separate from the crossing flock and return inland. Over the island of Malta, 824 honey-buzzards were observed, and we estimated the passage of 662 (80%) juveniles and 162 (20%) adults (Fig. 2B; 111 adults and 474 juveniles identified). The difference between the number of individuals belonging to the two age classes estimated at the two sites was significant among adults ($\chi^2 = 13.06$, $df = 1$, $P < 0.01$), but not among juveniles ($\chi^2 = 1.00$, $df = 1$, $P > 0.05$). Similar to Circeo promontory, the migratory flow over the island of Malta showed two pulses of movements, on 13 and 16–17 September, when 130 and 435 individuals were recorded, respectively (Fig. 3).

These results agree with those of the previous study made at these two sites (Agostini et al. 2002). We suggest that many honey-buzzards seen undertaking the crossing of the Tyrrhenian Sea heading toward the island of Ponza, probably deviated eastward to reach the Italian peninsula again, passing over Malta 2–5 d later. Based on our data and other observations (Kerlinger 1989), honey-buzzards seem to travel 350–500 km/d. However, during the

second week of September 2002, both in central and southern Italy, the weather was characterized by frequent rain because of the passage of low pressure cells. We suggest that because of these weather conditions, honey-buzzards took 5 d to cover about 750 km between Circeo and Malta.

To explain the tendency of juvenile honey-buzzards to undertake the crossing of the Tyrrhenian Sea, we have suggested that during their first migration, birds do not know the migratory routes and do not have experience with the higher energetic cost of flying over water (Agostini et al. 2002). Also, because many individuals observed at the Circeo promontory presumably belong to the breeding population in central Italy (Fig. 1), they are heavy with fat at the beginning of migration (Agostini et al. 2002). Finally, the geographic characteristics of the site could also play a role. At this point, the orientation of the coast changes, bending more easterly for ca. 60 km. Thus, the Circeo promontory, located in the southernmost point of the Pianura Pontina, appears as a natural springboard toward the sea. However, although the difference between number of juveniles recorded at the Circeo and over Malta was not significant, the analysis of the timing of passage seems to suggest that the birds used alternative migratory routes. During the peak passage (14–17 September) only about half of the birds counted over Malta were recorded at the Circeo promontory. Conversely, 262 birds were counted in central Italy between 18–30 September, but only 60 over Malta (Fig. 3). Also during autumn 2000, a marked difference was recorded between counts made at the two sites during the peak passage (21–24 September; Agostini et al. 2002). In particular, a total of 368 birds were seen over Malta, while only 237 individuals were counted at the Circeo promontory two days earlier. Apparently, some of the birds seen over Malta were not seen at the Circeo promontory. On the other hand, previous observations showed that at least some juvenile honey-buzzards reach Tunisia crossing this Mediterranean area via the islands of Capri and Marettimo (Fig. 1; Jonzén and Pettersson 1999, Agostini et al. 2002). Moreover, a recent study using satellite telemetry suggests that wind drift could affect this decision (crossing the Tyrrhenian Sea or not). In particular, juvenile honey-buzzards, like juvenile Ospreys (*Pandion haliaetus*), are susceptible to drift by crosswinds, whereas adults compensate and are less affected by wind (Thorup et al. 2003). Consequently, during easterly winds, juvenile birds that leave the Italian peninsula may be more likely to cross the Tyrrhenian Sea (Fig. 1).

During the second half of September 2002, observations on the migration of honey-buzzards were also made over Pianosa, a small island located about 40 km east of Corsica and 300 km northwest of the Circeo promontory (Fig. 1). At this site Paesani and Politi (2002) recorded 533 honey-buzzards en route to Corsica, nearly all (408) observed on 19 September. Because a similar late passage was not recorded over Circeo and Malta, these birds

probably reached Africa via the islands of Corsica and Sardinia (Fig. 1). This conclusion would agree with data reported by Thibault (1983) and Grussu (2001) concerning a late passage of flocks of honey-buzzards using the Corsica-Sardinia route (Fig. 1). The existence of two different responses among juveniles of this species when reaching water barriers (crossing the sea following the innate-migratory direction vs. following the coast), could explain why young honey-buzzards cross the Mediterranean Sea on a broader front than adults.

RESUMEN.—Durante la migración de otoño los juveniles europeos de *Pernis apivorus* tienden a emigrar dos semanas después de los adultos, concentrando su paso a través del mediterráneo después del 10 de septiembre. En el área del Mediterráneo central, cientos de juveniles de *Pernis apivorus* son observados en el promontorio del Circeo (Italia central) y sobre la Isla de Malta. Aquí probamos la sugerencia que las aves juveniles que llegan al Mar Mediterráneo siguen la península italiana y cruzan las aguas abiertas entre Sicilia y Libia con datos colectados en el promontorio de Circeo y Malta entre el 26 de Agosto y el 30 de Septiembre del 2002. En el promontorio de Circeo, 860 aves fueron contabilizadas con un estimado de 625 juveniles y con un pico entre 14–16 de Septiembre. Sobre Malta, 824 aves fueron contabilizadas incluyendo un estimado de 662 juveniles y con un pico entre 16–17 de Septiembre. Estos resultados surgieron que muchas de las aves contabilizadas en el promontorio de Circeo también pasan cerca de nuestro sitio de muestreo en Malta 2–3 días después. Aunque la diferencia entre el número de juveniles registrado en estos dos sitios no fue significativa, el análisis de las variaciones diarias del flujo de la migración parece sugerir que parte de las aves vistas en el promontorio Circeo no pasaron sobre Malta y tal vez cruzaron el Mar Tirreno. La existencia de dos estrategias diferentes usadas por los juveniles de estas especies para abordar las barreras acuáticas (cruzar el mar o seguir la costa) puede explicar el por qué los juveniles de esta especie tienden a cruzar el mar en un frente mas amplio que los adultos.

[Traducción de César Márquez]

ACKNOWLEDGMENTS

We are grateful to the Aeronautica Militare Italiana for permission to enter a military zone and to the Ente Nazionale Assistenza Volo for permission to use the roof of its building as an observation site. We thank J. Bednarz, N. Kjellén, P. Kerlinger, J. Seoane, and R. Yosef for their useful comments on earlier drafts of the manuscript.

LITERATURE CITED

- AGOSTINI, N. AND D. LOGOZZO. 1995. Autumn migration of honey-buzzards in southern Italy. *J. Raptor Res.* 29:275–277.
- AND ———. 1997. Autumn migration of Accipitriformes through Italy en route to Africa. *Avocetta* 21:174–179.

- , ———, AND C. COLEIRO. 1999. The orientation/navigation hypothesis: an indirect evidence in migrating honey buzzards. *Riv. Ital. Ornitol.* 69:153–159.
- , ———, AND M. PANUCCIO. 2000. The island of Marettimo, important bird area for the autumn migration of raptors. *Avocetta* 24:95–99.
- , C. COLEIRO, F. CORBI, G. DI LIETO, F. PINOS, AND M. PANUCCIO. 2002. Water-crossing tendency of juvenile honey buzzards (*Pernis apivorus*) during migration. *Avocetta* 26:41–43.
- BEAMAN, M. AND C. GALEA. 1974. Visible migration of raptors over the Maltese Islands. *Ibis* 116:419–431.
- BERTHOLD, P. 2001. Bird migration: a general survey. Oxford University Press, New York, NY U.S.A.
- CORBI, F., F. PINOS, M. TROTTA, G. DI LIETO, AND D. CASCIANELLI. 1999. La migrazione post-riproduttiva dei rapaci diurni nel promontorio del Circeo (Lazio). *Avocetta* 23:13.
- CRAMP, S. AND K.E.L. SIMMONS. 1980. The birds of the western Palearctic. Vol. 2. Oxford University Press, Oxford, U.K.
- GENSBØL, B. 1992. Guida ai rapaci diurni d'Europa, nord Africa e medio oriente. Zanichelli, Bologna, Italy.
- GRUSSU, M. 2001. Recenti avvistamenti. Periodo aprile 2000–maggio 2001. *Aves Ichnusae* 4:73–81.
- JONZÉN, N. AND J. PETTERSSON. 1999. Autumn migration of raptors on Capri. *Avocetta* 23:65–72.
- KERLINGER, P. 1989. Flight strategies of migrating hawks. University Chicago Press, Chicago, IL U.S.A.
- KJELLÉN, N. 1992. Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. *Ornis Scand.* 23:420–434.
- MARKS, J.S. AND R.L. REDMOND. 1994. Migration of Bristle-thighed Curlews on Laysan Island: timing, behavior and estimated flight range. *Condor* 96:316–330.
- PAESANI, G. AND P.M. POLITI. 2002. Monitoraggio della migrazione autunnale dei rapaci diurni nell'isola di Pianosa (LI). *Informamigrans* 10:6–7.
- SCHMID, H. 2000. Getrennte wege: der herbstzug von juvenilen und adulten wespenbussarden *Pernis apivorus*—eine synthese. *Ornithol. Beob.* 97:191–222.
- THIBAUT, J.C. 1983. Les oiseaux de la corse. Parc. Nat. Reg. De la Corse, Ajaccio, Corsica.
- THORUP, K., T. ALERSTAM, M. HAKE, AND N. KJELLÉN. 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proc. R. Soc. Lond.* 270:S8–S11.

Received 3 March 2003; accepted 23 April 2004

LETTERS

J. Raptor Res. 38(3):287–288

© 2004 The Raptor Research Foundation, Inc.

DO EURASIAN HOBBIES (*FALCO SUBBUTEO*) HAVE “FALSE EYES” ON THE NAPE?

We propose that the two whitish or creamy-colored spots on the nape of the Eurasian Hobby (*Falco subbuteo*; Fig. 1) are “false eyes” or ocelli, resembling a similar feature described for American Kestrels (*F. sparverius*; Clay 1953, *Wilson Bull.* 65:129–135). In both Eurasian Hobbies and American Kestrels, the “false eyes” confer an owl-like appearance to the individuals when viewed from the rear (Figs. 1 and 2). Even though hobbies have been extensively studied in Europe and their plumage patterns have been thoroughly described in raptor books and bird field guides, this is, to our knowledge, the first time that “false eyes” are hypothesized to be present in this species.

We examined preserved skins of Eurasian Hobbies from the Iberian Peninsula (Biological Station of Doñana, Sevilla, Spain, $N = 36$ specimens; National Museum of Natural Sciences at Madrid, Spain, $N = 16$ specimens) and Kazakhstan (Natural Sciences Museum of Kostanay, $N = 1$ specimen). We noted ocelli on live hobbies as well. In June 2003, J.J. Negro made observations of two captive birds from central Spain, seven individuals kept at the Almaty Zoo in Kazakhstan, and one free-ranging bird (observed using a spotting scope at a distance of ca. 50 m) at the Naurzum nature reserve in northern Kazakhstan. All these birds, including adults and juveniles, males and females, and originating from opposite ends of the species’ range in Eurasia, presented the two ocelli. These ocelli may have been overlooked in the literature because they are retractable and only fully visible when the occipital feathers are erect (based on observations of live birds). In museum specimens, the two ocelli are visible, and each marking covers an area of 0.2–0.8 cm², whereas on live birds, when fully displayed, the ocelli each cover an area of about 2.5 cm². These ocelli can be described as two rounded or elliptical light-colored spots located within the otherwise dark-gray plumage of the back of the head. The occurrence of these ocelli on nestlings and immatures (in both Eurasian Hobbies and American Kestrels) suggest that these “false eyes” are not sexually-selected traits and calls for alternative functional hypotheses.

In the case of the American Kestrel the function of the ocelli has not yet been established, although the subject has been debated for years. Clay (1953) suggested that the false eyes were “deflective” marks; in other words, patterns that are conspicuous in appearance and may misdirect the attack of potential enemies from the more to the less vital parts of the body (Cott 1940, *Adaptive coloration in animals*, Oxford University Press, New York, NY U.S.A.). Mueller (1971, *Wilson Bull.* 83:249–254) suggested that the head markings were used in the territorial displays of the species. Balgooyen (1975, *Jack-Pine Warbler* 53:115–116) advocated the protective function of the ocelli, but suggested they would be most important in this regard when the kestrels bow for eating or grooming, two situations in which the birds would be most vulnerable to attack by avian predators. Balgooyen (1975) suggested that the ocelli would give the illusion of watchful eyes and would make predators think that their potential prey had discovered them.



Figure 1. Eurasian Hobbies (*Falco subbuteo*) showing “false eyes” on the nape (from the collection of the National Museum of Natural Sciences at Madrid). The visual effect is more pronounced in live-mounted specimens with erected occipital feathers (two individuals to the right) compared to museum skins (four individuals to the left).

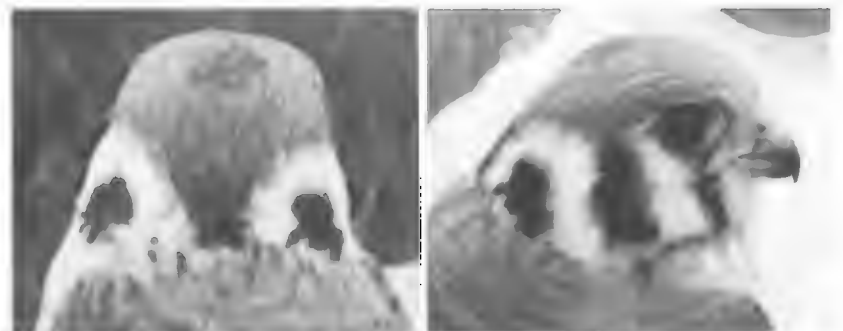


Figure 2. American Kestrel (*Falco sparverius*) in a posterior (left) or lateral (right) view, showing the ocelli in the nape.

Even though American Kestrels and Eurasian Hobbies live on different continents, they have common ancestry within the Falconiformes as they are congeneric (but not closest relatives; J. Figuerola pers. comm.). Given that two related species apparently have the same type of visual signal, we recommend a detailed comparison of ecological and behavioral characteristics of the two species. Such studies may prove fruitful in unraveling the evolution of a seemingly sophisticated trait, which has only been previously described in two genera of nocturnal predators, the pygmy owls of the genus *Glaucidium* (del Hoyo et al. 1994, Handbook of the birds of the world, Lynx Editions, Barcelona, Spain) and the Northern Hawk Owl (*Surnia uhula*; Svensson et al. 2001, Collins Bird Guide, Collins, U.K.). Field experiments using either stuffed or live birds, in which the ocelli can be covered at will by the experimenter, are needed to test the hypothesis that predators are deterred by the ocelli.

We thank Josefina Barreiro, José Cabot, and Evgeny Bragin for providing access to museum specimens. Arantxa, from Grupo para la Rehabilitación de la Fauna Autóctona y su Hábitat, lent us a live hobby for behavioral observations.—**Juan José Negro (negro@ebd.csic.es), Juan Manuel Grande, and José Hernán Sarasola, Department of Applied Biology, Estación Biológica de Doñana, Pabellón del Perú, Avda. M^aLuisa s/n, 41013 Seville, Spain.**

Received 2 April 2003; accepted 9 December 2003

Associate Editor: Joan L. Morrison

J. Raptor Res. 38(3):288–289

© 2004 The Raptor Research Foundation, Inc.

VULTURE WINTER ROOST ABANDONMENT AND REESTABLISHMENT

Turkey Vultures (*Cathartes aura*) and Black Vultures (*Coragyps atratus*) often roost communally in large, mixed-species groups during winter. Use of a traditional roost located at the base of Big Round Top (BRT) hill in Gettysburg National Military Park, Gettysburg, PA (Adams County), by wintering vultures has been well documented for many years (Wright et al. 1986, *J. Raptor Res.* 20:102–107; Thompson et al. 1990, *J. Wildl. Manage.* 54:77–83). The BRT roost consists of several mature white pine (*Pinus strobus*) trees and various hardwood trees located on a southeast-facing slope in the approximate center of the forest stand at BRT hill. We sought to determine the status of the BRT roost and another roost that apparently has been established recently in the vicinity of the BRT roost. The new roost is at Lake Heritage (LH), a gated community about 7 km from the BRT roost, that consists of two distinct clumps of coniferous trees ca. 0.5 km apart within a residential area. One clump contains 12 scotch pines (*Pinus sylvestris*) and the other clump consists of five white pines (Roén 2002, Habitat use and feeding behavior of avian scavengers in Gettysburg National Military Park, M.S. thesis, Pennsylvania State Univ., University Park, PA U.S.A.).

We assessed vulture use of both roosts in winter by monitoring individuals leaving the roosts during early morning hours. We conducted 19 counts at the BRT roost; observations were made from an elevated position 280 m from the roost location (Wright et al. 1986). Counts occurred 1–4 d/wk from December 1999–March 2000 and four times from December 2000–March 2001 (Roén 2002). Counts were not conducted on days with measurable precipitation or dense fog. Each count began 30 min prior to sunrise and continued for 60–90 min.

We first suspected that vultures were present at the LH roost in 1999 because of the large number of vultures (>80) observed circling over the residential community at dusk. Subsequently, we counted vultures at the LH roost 1–3 d/wk from December 2000–March 2001 from a vehicle 30–60 m from each distinct clump of trees (referred to as Jackson and Longstreet after the bordering street names), for a total of 14 counts. Beginning 30 min before dawn, we counted vultures leaving the Jackson clump for 30 min, then we counted vultures remaining on the roost. Next, we traveled by vehicle to the Longstreet clump and conducted our counts there for an additional 60 min or until all vultures had exited the roost trees. This method most likely resulted in an underestimate of the total number of roosting vultures because some vultures may have exited the Longstreet roost trees while we were at the Jackson location. We often observed vultures moving from the Longstreet clump to the Jackson clump, but never observed the reverse. Therefore, some vultures were included in our count as they exited the Jackson trees after previously roosting at the Longstreet location.

We never observed vultures using the BRT roost during any of our counts there. Historically, numbers of vultures at this roost ranged from a mean of 199 over seven counts in late winter 1983 to a mean of 719 over 15 counts in mid-winter 1983 (Wright et al. 1986). Thompson et al. (1990) reported a mean of 665 roosting vultures at BRT over

four counts conducted during the 1986 and 1987 winter seasons. Based on these studies, anecdotal evidence provided by National Park Service personnel (H. Greenley pers. comm.), and the absence of vultures from this roost during our counts in 1999–2001, we believe the BRT roost was abandoned by wintering vultures sometime between 1988 and 1999.

We observed vultures using the LH roost during each of the 14 counts conducted in 2000–01. The number of Turkey Vultures observed per count ranged from 42–157 individuals (\bar{x} = 96, SE = 9) and the number of Black Vultures recorded per count ranged from 9–101 individuals (\bar{x} = 34, SE = 8).

Based on possible factors given for a decline in vulture numbers at other roosts (Taylor 1986, *Great Basin Nat.* 46:305–306) we identified several factors possibly contributing to the apparent abandonment of the BRT roost and subsequent establishment of the LH roost. These include (1) a possible regional decline in vulture population numbers, (2) land-use changes in the vicinity of Gettysburg National Military Park and at the county level, (3) changes in food availability at the BRT roost, and (4) possible impacts of increased disturbance at the BRT roost.

Although some studies have reported a general decline in vulture numbers in the eastern United States (e.g., Tate and Tate 1982, *Am. Birds* 36:126–135), more recent studies have reported an increase (McWilliams and Brauning 2000, *The birds of Pennsylvania*, Comstock Publication Associates, Ithaca, NY U.S.A.). We often observed vultures foraging within 500 m of the BRT roost in winter, despite a lack of vultures using the roost. Although no evidence currently exists for a regional decline in vulture numbers, such a decline, even if it exists, would not explain why vultures abandoned the BRT roost while using the LH roost.

Substantial land-use changes have occurred recently within Adams County, including the building of an outlet mall in 1999, other commercial buildings, and numerous residences within 5 km of the BRT roost. In Adams County, the number of farms decreased by 11% between 1987 and 1997, and the amount of farmland dropped from 75 723 ha to 72 381 ha during the same time period (National Agriculture Statistics Service 1999, 1997 Census of agriculture: geographic area series, Vol. 1, 1A, 1B, 1C, US Department of Agriculture, Washington, DC U.S.A.). Given the close proximity of the LH roost to the abandoned BRT roost and the large home ranges of vultures (Coleman and Fraser 1989, *J. Wildl. Manage.* 53:782–792), we believe that such land-use changes would similarly impact vultures roosting at both sites. Thus, local land use changes would not explain why vultures abandoned the BRT roost while using the LH roost.

Food availability near the BRT roost may have been affected by the efforts of staff at Gettysburg Park to reduce populations of white-tailed deer (*Odocoileus virginianus*). In response to high deer densities at Gettysburg, park managers initiated a shooting program in 1995 (National Park Service 1995, Management guidelines for white-tailed deer reduction—Gettysburg National Military Park and Eisenhower National Historic Site, USDI, Washington, DC U.S.A.), which removed a total of 1495 deer over a 7-yr period (Z. Bolitho pers. comm.). Because road-killed deer comprise a portion of vulture diets (Coleman and Fraser 1987, *J. Wildl. Manage.* 51:733–739; Yahner et al. 1990, *J. Wildl. Manage.* 54:77–83), fewer deer in Gettysburg Park likely led to fewer incidences of vehicle-deer collisions and, hence, the amount of food available to vultures.

Increased levels of disturbance at the BRT roost could have contributed to roost abandonment. Shooting associated with the deer-reduction program occurred at night between October and March each year (National Park Service 1995), which coincides with the months vultures spend at the roosts (McWilliams and Brauning 2000). Shooting occurred throughout the park, including near BRT hill and the immediate vicinity (Z. Bolitho pers. comm.). Increased visitorship at Gettysburg Park could have caused additional disturbance to the roost. The total annual number of visitors to the park increased 40% between 1982 and 1999, and visitorship during winter has risen 25% from 1982–2000 (National Park Service unpubl. data).

Limited information exists regarding the use and dynamics of vulture winter communal roosts (T.M. Sweeney and J.D. Fraser 1986, *Wildl. Soc. Bull.* 14:49–54; Wright et al. 1986; Thompson et al. 1990). We have documented the abandonment of a historic roost at BRT and establishment of a new roost at LH. It is important to note that this change in roost location occurred; however, we only have limited data regarding use of the new roost. Clearly, further study is needed to assess possible causes of roost abandonment, and the establishment and use of new roosts by wintering vultures.

This study was supported by the National Park Service and the Pennsylvania Agricultural Experiment Station. We thank the staff of Gettysburg National Military Park, especially Z. Bolitho, H. Frost, C. Musselman, R. Krichten, and B. Thompson. Field assistance was provided by V. Sauter, K. Field, J. Williams, M. Swartz, G. Roen, and E. Rehm — **Keely T. Roen (e-mail address: kat175@psu.edu) and Richard H. Yahner, Intercollege Graduate Degree Program in Ecology and School of Forest Resources, Pennsylvania State University, University Park, PA 16802 U.S.A. Present address for K.T. Roen: Wildlife Technology Program, Pennsylvania State University, DuBois Campus, DuBois, PA 15801 U.S.A.**

Received 15 January 2003; accepted 28 May 2004

Associate Editor: Joan L. Morrison

J. Raptor Res. 38(3):290

© 2004 The Raptor Research Foundation, Inc.

COMMENSAL FORAGING BY A RED-SHOULDERED HAWK (*BUTEO LINEATUS*) WITH WILD TURKEYS (*MELEAGRIS GALLOPAVO*)

On 6 August 2003, I observed an instance of commensal foraging by a Red-shouldered Hawk (*Buteo lineatus*) with Wild Turkeys (*Meleagris gallopavo*). I began watching a flock of 15 adult turkeys at 0745 H from a distance of 250 m (through 10 × 40 binoculars) as they foraged in a weedy, grazed pasture bordered by an oak-hickory (*Quercus-Carya*) woodlot near the mouth of Crooked Creek on the White River, Marion County, Arkansas (36°13.6'N, 92°28'W). At 0900 H a juvenile Red-shouldered Hawk flew across the pasture toward the turkeys and perched on a low branch at the forest edge. As the hawk approached, the turkeys cackled and ran into the forest but all emerged from cover within 1–2 min and resumed feeding in the pasture some 5–15 m from the forest edge. Over the next 90 min, the hawk followed the turkeys as they meandered 225 m southward along the ecotone. On five occasions the hawk dropped to the ground from a low perch (2–4 m above ground) at the edge of the woodlot to capture small prey items with its talons. After consuming the prey on the ground, the hawk would walk a few steps, pause, and then fly to another perch within 5–8 m of the leading front of the turkey flock. The turkeys showed little reaction to the hawk except for one hen, which feigned a lunge toward the hawk on the ground from ca. 5 m away. The observations ended when the turkeys and hawk moved out of sight around a bend of the woodlot.

About an hour later, I followed the path of the turkeys and found grasshoppers (primarily *Syrbula admirabilis*, *Arphia simplex*, *Cortophaga viridifasciata*, *Hippiscus ocelote*, and *Dissosteira carolina*) to be fairly abundant in the pasture. It seems probable that the hawk was feeding on grasshoppers flushed by the turkeys. This observation appears to be the first report of commensal foraging by the Red-shouldered Hawk (Crocoll 1994, *In* A. Poole and F. Gill [Eds.], *The birds of North America*, No. 107. The Academy of Natural Sciences and American Ornithologists' Union, Washington, DC U.S.A.). I thank Bill Pranty, Michael McCrary, and Jerry Mastel for comments on the manuscript and Bob Yeider for hospitality on the White River.—**Gary R. Graves** (e-mail address: graves.gary@nsmnh.si.edu), Department of Zoology, MRC-116, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, DC 20013 U.S.A.

Received 5 September 2003; accepted 21 March 2004

Associate Editor: Michael I. Goldstein

J. Raptor Res. 38(3):290–292

© 2004 The Raptor Research Foundation, Inc.

NOTES ON A RANGE EXPANSION AND SUMMER DIET OF THE MOUNTAIN CARACARA IN THE ANDES OF SOUTH-CENTRAL CHILE

The Mountain Caracara (*Phalcoboenus megalopterus*) ranges from sea level to 5000 m in Perú, Bolivia, northwestern Argentina, and Chile (Araya and Millie 1996, *Guía de campo de las aves de Chile*, 7th Ed., Editorial Univer., Santiago, Chile; González and Malaga 1997, *Ornithol. Neotrop.* 8:57–69). Although the species is known to inhabit much of Chile (18–33°S; Araya and Millie 1996), the southern limit of its distribution is unclear in the literature. Based on a bird collected by Bridges in 1843 (Fraser 1843, *Proc. Zool. Soc. Lond.* 11:108–121), various authors list the Mountain Caracara's southern-range limit as Colchagua (34°35'S, 71°24'W; Hellmayr 1932, *Birds of Chile*, *Field Mus. Nat. Hist. Publ., Zool. Ser.* 10:1–472, Goodall et al. 1951, *Aves de Chile*, Vol. 2, Platt Editores Gráficos, Buenos Aires, Argentina). The Bridges' collection site is not exactly known, but it has been assumed to be the Colchagua Province (Paynter 1988, *Ornithological Gazetteer of Chile*, Mus. Comp. Zool. Harvard Univ., Cambridge, MA U.S.A.). Following Philippi (1964, *Invest. Zool. Chil.* 11:1–74), other authors have extended the southern limit of the Mountain Caracara's range south to Talca (Johnson 1965, *The birds of Chile*, Vol. 2, Establ. Gráficos, Buenos Aires, Argentina; Fjeldså and Krabbe 1990, *Birds of the high Andes*, Appolo Books, Svendborg, Denmark). Philippi (1964), however, does not

explain the rationale for this extension, and it is not clear if he refers to the city of Talca (32°25'S, 71°40'W) or the province (34–35°S, 70–72°W).

Recently, Figueroa et al. (2000, *Bol. Chil. Ornitol.* 7:2–12) recorded the Mountain Caracara in the Huemules del Niblinto Nature Sanctuary and National Reserve (henceforth, Niblinto Sanctuary; 36°45'S, 71°30'W) near Nevados de Chillán in the Andes mountain range, ca. 140 km south of the southern boundary of Talca province. This record potentially represents a new southern limit of the distribution of the Mountain Caracara. Figueroa et al. (2000) mentioned that the caracaras were recorded in the vicinity of Baul Mountain (36°44'56"S, 71°29'12"W), but did not give details about those observations.

Here, we describe observations of Mountain Caracaras made during three consecutive years in the same area studied by Figueroa et al. (2000). Niblinto Sanctuary is a rugged area ca. 10 000 ha in size, with elevations ranging from 800–2200 m and slopes up to 45°. Topography includes valleys, plateaus, and numerous ridges dissected by deep ravines that carry water during winter and spring. The vegetation is composed primarily of mixed-deciduous *Nothofagus* forests and shrublands characterized by a diversity of high-Andean species (Figueroa et al. 2000). The Niblinto Sanctuary is a jointly managed private/public wildlife protected area forming part of the Nevados de Chillán, a priority site for biodiversity conservation in Chile (Muñoz et al. 1996, Libro rojo de los sitios prioritarios para la conservación de la diversidad biológica en Chile, Corporación Nacional Forestal, Santiago, Chile).

On 26 February 2001, two adult Mountain Caracaras were seen around Baul Mountain in the Niblinto Sanctuary. The next day, a juvenile Mountain Caracara (identified by plumage; Brown and Amadon 1968, *Eagles, hawks and falcons of the world*, Vol. 1, Country Life Books, London, U.K.) was seen in the same area. On 29 January 2002, two adult Mountain Caracaras were perched on the north slope of Colchon Mountain, 5 km southwest of Baul Mountain. On the same day, two adult Mountain Caracaras were also observed near Las Yeguas Mountain, 4 km northeast of Colchon Mountain and 3 km northwest of Baul. On 23 February 2002, two adults were seen chasing a juvenile around Baul Mountain. More recently, on 2 February 2003, one adult Mountain Caracara was seen near Baul Mountain.

Because only one or two individual Mountain Caracaras were observed at each sighting, we are not sure if more than one pair occurred at our study site. Diurnal raptors frequently exhibit long local movements (Newton 1979, *Population ecology of raptors*, T. & A.D. Poyser, London, U.K.) and so our records may correspond to only one pair. Even so, we believe that sightings of the Mountain Caracara obtained during three consecutive yr in the Niblinto Sanctuary are sufficient evidence to extend the species' southern distributional range. Including these records of the Mountain Caracara, a total of 12 diurnal and four nocturnal raptors have been recorded in the Niblinto Sanctuary (Figueroa et al. 2000), supporting the importance of this site for the conservation of Andean biodiversity (Muñoz et al. 1996).

During our study period in the Niblinto Sanctuary, we also obtained limited information on the diet of Mountain Caracaras. From 24–28 February 2001, we collected 20 pellets below a cliff on Baul Mountain, where a Mountain Caracara pair was observed roosting. We observed the roosting site from dawn to sunset (0700–2100 H) for all 5 d using a telescope (60×) and binoculars, and pellets were collected every morning or afternoon. During this period, no other raptors were observed on the cliff. The Mountain Caracara's pellets were similar in appearance to pellets of the Chimango Caracara (*Milvago chimango*) and Crested Caracara (*Polyborus plancus*; pers. obs.). Pellets were dissected in the laboratory using forceps to separate all prey remains. Because most of the pellets were broken, we were unable to obtain quantitative information on diet; however, we attempted to identify prey remains and thus develop a qualitative description of the diet of this Mountain Caracara pair.

Of all prey items identified ($N = 54$), most were insects (94%; identified by head capsules and elytra). Coleopterans (genera: *Epipedonata*, *Ectinogonia*, *Polycesta*, *Tibionema*, *Ryephene*, *Sphenognathus*, *Aegorhinus*) predominated (89%), although some Orthopterans (*Aucacris* spp.) were noted (5%). The Plain-mantled Tit-Spinetail (*Leptasthenura aegithaloides*; identified by feathers), an unidentified bird, and the great rock rat (*Aconaemys fuscus*; identified by skull) were the only vertebrate species detected, each accounting for 2% of the prey items recorded. The large number of terrestrial insects found in the pellets is consistent with the Mountain Caracara's foraging habits. This species is adept at ground foraging, scratching, and stamping to disturb insects living underground or beneath rocks (Jones 1999, *Wilson Bull.* 11:437–439).

Although our information is limited, our results are similar to information on this raptor's diet reported by others (Johnson 1965, Brown and Amadon 1968). To our knowledge, however, no study has used pellets to assess diet of this species. Perhaps, pellets are difficult to find because areas typically inhabited by Mountain Caracaras are rugged and inaccessible. Because our data are based on a small and geographically-limited sample, further investigation is necessary to understand the food habits of this little known caracara.

This publication is part of the Huemul Deer Conservation Project financed by the Zoological Society of Frankfurt of the Comité Pro Defensa de la Fauna y la Flora, Chile, and of the Andean Raptors project financed with private funds. We thank Rodrigo López who provided support, Diane Haughney for helping us with the English translation, and Benito González, Roberto Schlatter, and Rodolfo Figueroa for supporting our work. Collection of field data was

made possible by the collaboration of Alberto Trostel, Juan Sepúlveda, Loreto Gómez, and Ishbak Shehadeh. Three anonymous referees helped improve the manuscript.—**Ricardo Figueroa Rojas** (e-mail address: asio@tie.cl), **Sergio Alvarado Orellana**, and **E. Soraya Corales Stappung**, **Estudios para la Conservación y Manejo de la Vida Silvestre Consultores, Blanco Encalada 350, Chillán, Chile.**

Received 13 November 2002; accepted 27 December 2003

Associate Editor: Joan L. Morrison

J. Raptor Res. 38(3):292–293

© 2004 The Raptor Research Foundation, Inc.

AN EXAMPLE OF COOPERATIVE HUNTING BY SAKER FALCONS IN HUNGARY

Cooperative or social hunting has been described for several diurnal raptors, including Sooty Falcons (*Falco coloratus*), Eleonora's Falcons (*F. eleonora*) (Walter 1979, Eleonora's Falcon: adaptations to prey and habitat in a social raptor. University Chicago Press, Chicago, IL U.S.A.), and Harris' Hawks (*Parabuteo unicinctus*; Mader 1976, *Living Birds* 14:59–85; Bednarz 1995, Harris' Hawk [*Parabuteo unicinctus*]. In A. Poole and F. Gill [Eds.], *The birds of North America*, No. 146. The Birds of North America, Inc., Philadelphia, PA U.S.A.). The strategy involves a pair hunting together, with one bird flying ahead to flush or disrupt the prey and the other usually following behind to capture the prey. Some social species group or flock-hunt cooperatively (Ellis et al. 1993, *BioScience* 43:14–20). Lanner Falcons (*F. biarmicus*), Brown Falcons (*F. berigora*), and Aplomado Falcons (*F. femoralis*) have been observed hunting in cooperative pairs (Hector 1986, *Ethology* 73:247–257; Mooney 1989, *Corella* 13:18–21; Leonardi 1999, *J. Raptor Res.* 33: 123–127), but the strategy is poorly documented for other large falconids such as the Saker Falcon (*F. cherrug*). Based on our review of literature only Gorman (1998, *Buteo* 10:103–104), reported observations that suggested possible cooperative hunting by sakers.

Sakers feed mainly on small mammals, but also take a variety of birds and other animals (Cade 1982, *The falcons of the world*. Comstock/Cornell University Press, Ithaca, NY U.S.A.). In Hungary, sakers forage largely on feral pigeons (*Columba livia*) and ground squirrels (Susliks, *Spermophilus citellus*), and often nest on artificial boxes and platforms recently placed on electrical towers (Bagyura et al. 1994, Pages 391–395 in B.-U. Meyburg and R.D. Chancellor [Eds.], *Raptor conservation today*. World Working Group on Birds of Prey, Berlin, Germany; Bagyura et al. 1994, Pages 397–401 in B.-U. Meyburg and R.D. Chancellor [Eds.], *Raptor conservation today*. World Working Group on Birds of Prey, Berlin, Germany; Baumgart 2000, Pages 295–299 in R.D. Chancellor and B.-U. Meyburg [Eds.], *Raptors at risk*. World Working Group on Birds of Prey, Berlin, Germany). Regardless of prey, sakers catch most of their prey on or near the ground and are generally less aerial hunters than Peregrine Falcons (*F. peregrinus*) or Gyrfalcons (*F. rusticolus*; Cade 1982). Sakers typically hunt from an elevated perch providing a commanding view of the terrain, then launch after prey, flying rapidly close to the ground, and capture prey on the ground. Sakers will also hover briefly like a large kestrel, particularly when searching for prey that has taken cover (Clark 1999, *A field guide to the raptors of Europe, the Middle East, and North Africa*. Oxford University Press, New York, NY U.S.A.; Forsman 1999, *The raptors of Europe and the Middle East: a handbook of field identification*. T. & A.D. Poyser, London, U.K.).

On 28 May 2003 at 0900 H local time, we observed one adult male and female saker (a breeding pair that later fledged two young; I. Sándor pers. comm.) 400 m away perched together on a 40 m electrical tower with a nesting platform in Hortobágy National Park, 35 km west of Debrecen in northeastern Hungary. After 10 min of observation the larger female flew west, followed immediately by the smaller male <3 sec later. Both sakers flew rapidly <50 m above ground level toward a cornfield <1 km distant. The female, first to arrive, dove to the ground and flushed a female Ring-necked Pheasant (*Phasianus colchicus*), which quickly dropped back into the field after the male made a subsequent passing attack. Both sakers hovered and made multiple dives for <20 sec at the location where the pheasant landed, again without making apparent contact, and then landed together on the ground, at which point both falcons and prey were out of view. Less than 30 sec later the pheasant became airborne (<5 m) briefly once again and was chased to the ground out of view by one of the falcons (sex undetermined).

Approximately one min later, an adult male Marsh Harrier (*Circus aeruginosus*) flew <10 m over the area and was chased by one of the sakers. The harrier landed on a low pile of cow dung and hay about 75-m away and the saker

returned to the presumed kill site. After 5 min, we drove to the cornfield and slowly approached the area by car. About 10 m from the kill site both falcons were spotted on the ground, then flushed and flew east, vocalizing. The bird on the pheasant appeared larger (female) with the smaller falcon close by. We approached the site on foot and verified that the pheasant had been killed and was partially consumed.

Cooperative hunting by sakers in Hungary has been reported by some observers (I. Sándor, M. Dudás, and J. Bagyura pers. comm.). However, it is unclear if these observations represented true cooperative hunting in which falcon pairs act together for mutual benefits or pseudo-cooperative hunting in which individual falcons pursue the same prey item independently (Ellis et al. 1993). Sakers in Hungary have been observed pair hunting, pursuing, and capturing pigeons (*Columba* spp.) and shorebirds (*Scolopacidae*) in what suggested true cooperative hunting (Gorman 1998). Our observations appear to support Gorman's (1998) suggestion that pairs of Saker Falcons employ cooperative hunting tactics successfully, but more data are needed to determine whether cooperative hunting occurs commonly in this species.

Travis L. Booms, Tom J. Cade, Iván Demeter, David H. Ellis, and Nick Fox provided critical comments on earlier drafts of the manuscript.—**Wade L. Eakle** (e-mail address: Wade.L.Eakle@spd02.usace.army.mil), U.S. Army Corps of Engineers, South Pacific Division, 333 Market Street, San Francisco, CA 94105 U.S.A.; **Carl Millier**, Falcon Environmental Services, C.P. 81, Ste-Anne-de-Bellevue, Québec H9X 3L4, Canada; **Pierre Mineau**, Canadian Wildlife Service, National Wildlife Research Center, Carleton University Campus, Raven Road, Ottawa, Ontario K1A 0H3, Canada; and **János Világosi**, Aquila Nature Tours, Péterfia u. 46. 2/11, H-4026 Debrecen, Hungary.

Received 9 September 2003; accepted 12 March 2004

BOOK REVIEW

J Raptor Res. 38(3):294

© 2004 The Raptor Research Foundation, Inc.

A Hawk in the Sun: Adventures Studying Hawks.

By Leon R. Powers. 2003. Dimi Press, Salem, OR U.S.A. xvi + 190 pp., 6 color photos, numerous line drawings. ISBN 0-931625-40-8. Paper, \$14.95.—This book relates Leon Powers' experiences studying Ferruginous Hawks (*Buteo regalis*) in northwestern Utah and adjacent Idaho from 1972 to 1974. The Ph.D. project was supervised by Chuck Trost at Idaho State University. Rich Howard began a companion study of the hawks' basic ecology and is prominently mentioned as a friend and research collaborator, as is Tim Craig, a volunteer assistant.

The objective was to document thermoregulatory adaptations that enable Ferruginous Hawks to survive in this hot desert environment. The approach included observations from a blind and the use of time-lapse cameras and temperature-sensitive transmitters, which was cutting-edge technology, as the author calls it, for that time.

Even though I have studied Ferruginous Hawks for about 20 yr, I found many new things in this book. I kept coming back to the pages to find out how the coordinated nest defense against a coyote would end, how adults and young coped with 108°F (42.4°C) heat at the northern fringe of the Great Basin, whether Ferruginous Hawks hunt during moonlit nights, and so on. I learned that males share in incubation, but otherwise do not dawdle at the nest; that females discard leftover prey and, surprisingly, pellets some 100–300 m from the nest; that the hawks cache food, and more. There is a heartbreaking description of a female losing the battle over her nestlings against a coyote while her mate was away, presumably hunting.

The book is enlivened by handsome drawings and photos. There are no tables, very few numbers, and few references. The ideas presented and the research described did not follow a hypothesis-testing approach, but were more akin to a naturalist's inquiry. This approach is deliberate.

A nagging fear permeates the presentation: the concern that observations from a blind >100 m away may cause nest failure. Powers repeatedly refers to Ferruginous Hawks as sensitive to disturbance. However, knowing that the hawks' tolerated his entering and staying in an observation blind—only some of the time accompanied by a second person walking away—suggests otherwise. What the hawks apparently found less tolerable was the time-lapse cameras about 8 m away. The author relates one event where the male made three prey deliveries after the camera was installed, but the female refused to return to feed her young by nightfall. One chick perished, and the death of the others was narrowly avoided through good judgment on the author's part. I suspect, individual differences aside, that many other North American raptors would be equally prone to desertion under the circumstances.

The writing style is direct and “from the heart.” Straightforward reporting is interspersed with vivid prose stimulating the reader's imagination. However, parts of the book suggest a cursory attention to the literature. For example, contrary to the author's assertion, courtship behavior has been described, albeit briefly, and large-area population estimates with random sampling have been carried out in Alberta and North Dakota (Bechard and Schmutz 1995, Ferruginous Hawk (*Buteo regalis*). In A. Poole and F. Gill [Eds.], *The birds of North America*, No. 172. The Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, DC U.S.A.). Ferruginous Hawk band recoveries are not universally of the one-in-one hundred ratio, but 3.7% in one study (Schmutz and Fyfe 1987, *Condor* 89:169–174), and even higher in others.

Notwithstanding these minor blemishes, the book is enjoyable and informative. Leon Powers states that “If you are one whose heart can still be stirred by the presence of wild things or by the sight of remote, wild landscapes, then perhaps I have written this story for you.”—**Josef K. Schmutz, Centre for Studies in Agriculture, Law and the Environment, University of Saskatchewan, Saskatoon, SK S7N 5A8 Canada.**



Buteo Books

Specializing in Ornithology

Toll Free: 800-722-2460

phone: 434-263-8671

fax: 434-263-4842

Buteo Books is the largest retailer of Ornithology books in North America, with over 2,000 in-print titles, and hundreds of out-of-print titles available.

A FEW BOOKS ON BIRDS OF PREY AND FALCONRY

Raptors of Eastern North America. Brian Wheeler.

Raptors of Western North America. Brian Wheeler.

Suggested Practices for Raptor Protection on Power Lines: State of the Art in 1996.

Return of the Peregrine: A North American Saga of Tenacity and Teamwork.

Tom Cade and William Burnham. The Peregrine Fund.

Birds of Prey: Health and Disease. Third Edition. John E. Cooper.

North American Falconry and Hunting Hawks, Eighth edition. Beebe & Webster.

Handbook of the Birds of the World. The first eight volumes of this projected sixteen-volume work are available for \$195 each. Volume 2 includes diurnal raptors, Volume 3 includes owls. Volume 9 will be available August 2004.

RARE AND OUT-OF-PRINT ORNITHOLOGY

Buteo Books has a wide selection of used and out-of-print titles available, including rare falconry collections. Our stock changes daily, so call to check availability of that scarce title you're seeking.

BIRDS OF NORTH AMERICA SERIES

This series consists of individual species accounts for each of the more than 700 species which breed in the United States and Canada, including diurnal and nocturnal raptors. These illustrated reviews provide comprehensive summaries of the current knowledge of each species, with range maps and extensive list of references.

Buteo Books is pleased to offer these accounts for \$7.50 each. All 716 profiles are listed in taxonomic order on our website. Singles may be ordered by contacting Buteo Books. Shipping and handling is \$4 for the first profile and \$1 for each additional profile to a maximum of \$10 per order.

Buteo Books; 3130 Laurel Road; Shipman, VA 22971; USA

Visit our website for more information:

www.buteobooks.com

A Telemetry Receiver Designed with The Researcher in Mind

What you've been waiting for!

Finally, a highly sensitive 999 channel synthesized telemetry receiver that weighs less than 13 ounces, is completely user programmable and offers variable scan rates over all frequencies. For each animal being tracked, the large LCD display provides not only the frequency (to 100Hz) and channel number, but also a 7 character alphanumeric comment field and a digital signal strength meter. Stop carrying receivers that are the size of a lunch box or cost over \$1500. The features and performance of the new R-1000 pocket sized telemetry receiver will impress you, and the price will convince you.

Other Features Include:

- Factory tuned to any 4MHz wide segment in the 148-174MHz Band • Very high sensitivity of -148dBm to -150dBm • Illuminated display and keypad for use in low light or darkness • User selectable scan rates from 1-30 seconds in 1 second steps • Rechargeable batteries operate the receiver for 12 hours and can be replaced with standard AA Alkaline batteries in the field. Both 12vdc and 110vac chargers are included.

- 6.1" (15.5cm) high,
2.6" (6.6cm) wide,
1.5" (3.8cm) deep.

- 3 year warranty
- 1 day delivery

\$695.00

Please specify desired 4MHz
wide segment in the
148-174MHz band

Visit our
website for
complete
specifications,
operating
manual and
information
on the R-1000
or call our
toll-free number
to order your
receiver now.

**Try the
New R-1000
and You'll Be
Impressed!**



COMMUNICATIONS SPECIALISTS, INC.

426 West Taft Avenue • Orange, CA 92865-4296 • 1-714-998-3021 • Fax 1-714-974-3420
Entire U.S.A. (800) 854-0547 • Fax (800) 850-0547 • <http://www.com-spec.com>



2004 ANNUAL MEETING

The Raptor Research Foundation, Inc. 2004 annual meeting will be held on 9–13 November 2004 in Bakersfield, California. For information about the meeting see the following website: http://www.calhawkingclub.org/field_meet/34th_annual/ or contact Rick Holderman (parabuteo1@cox.net).

Persons interested in predatory birds are invited to join The Raptor Research Foundation, Inc. (see: <http://biology.boisestate.edu/raptor/>). Send requests for information concerning membership, subscriptions, special publications, or change of address to OSNA, P.O. Box 1897, Lawrence, KS 66044-8897, U.S.A.

The Journal of Raptor Research (ISSN 0892-1016) is published quarterly and available to individuals for \$33.00 per year and to libraries and institutions for \$50.00 per year from The Raptor Research Foundation, Inc., 14377 117th Street South, Hastings, Minnesota 55033, U.S.A. (Add \$3 for destinations outside of the continental United States.) Periodicals postage paid at Hastings, Minnesota, and additional mailing offices. POSTMASTER: Send address changes to *The Journal of Raptor Research*, OSNA, P.O. Box 1897, Lawrence, KS 66044-8897, U.S.A.

Printed by Allen Press, Inc., Lawrence, Kansas, U.S.A.

Copyright 2004 by The Raptor Research Foundation, Inc. Printed in U.S.A.

⊙ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

RAPTOR RESEARCH FOUNDATION, INC.

Grants and Awards

For details and additional information visit: <http://biology.boisestate.edu/raptor/rrfi.htm>

Awards for Recognition of Significant Contributions.

The **Tom Cade Award** is a non-monetary award that recognizes an individual who has made significant advances in the area of captive propagation and reintroduction of raptors. The **Fran and Frederick Hamerstrom Award** is a non-monetary award that recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Submit nominations for either award to: Dr. Clint Boal, Texas Cooperative Fish and Wildlife Research Unit, BRD/USGS, Texas Tech University, 15th Street & Boston, Ag Science Bldg., Room 218, Lubbock TX 79409-2120 U.S.A.; phone: 806-742-2851; e-mail: cboal@ttu.edu

Awards for Student Recognition and Travel Assistance.

The **James R. Koplin Travel Award** is given to a student who is the senior author and presenter of a paper or poster to be presented at the RRF meeting for which travel funds are requested. Application deadline: due date for meeting abstract. Contact: Dr. Patricia A. Hall, 5937 E. Abbey Rd., Flagstaff, AZ 86004; phone: 520-526-6222 U.S.A.; e-mail: pah@spruce.for.nau.edu

The **William C. Anderson Memorial Award** is given to both the best student oral and poster presentation at the annual RRF meeting. The paper cannot be part of an organized symposium to be considered. Application deadline: due date for meeting abstract, no special application is needed. Contact: Rick Gerhardt, Sage Science, 319 SE Woodside Ct., Madras, OR 97741 U.S.A.; phone: 541-475-4330; email: rgerhardt@madras.net

Grants.

Application deadline for all grants is February 15 of each year; selections will be made by April 15.

The **Dean Amadon Grant** for up to \$1000 is designed to assist persons working in the area of systematics (taxonomy) and distribution of raptors. The **Stephen R. Tully Memorial Grant** for up to \$500 is given to support research and conservation of raptors, especially to students and amateurs with limited access to alternative funding. Agency proposals are not accepted. Contact for both grants: Dr. Carole Griffiths, 251 Martling Ave., Tarrytown, NY 10591 U.S.A.; phone: 914-631-2911; e-mail: cgriff@liu.edu

The **Leslie Brown Memorial Grant** for up to \$1400 is given to support research and/or the dissemination of information on African raptors. Contact: Dr. Jeffrey L. Lincer, 9251 Golondrina Drive, La Mesa, CA 91941, U.S.A.; e-mail: JeffLincer@tns.net